

MALAYSIAN PARASITES IX
NOTES ON THE TAXONOMY OF TROMBICULID MITES
WITH DESCRIPTION OF A NEW SUBGENUS

By
J. R. AUDY

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The most comprehensive accounts of the taxonomy of the trombiculids are the excellent and timely monographs published during 1952 by Womersley, by Wharton & Fuller, and by Fuller. Wharton, aided by Fuller, has published an invaluable manual, the taxonomic part of which had however to be completed immediately before a spate of new species were described and without access to Womersley's simultaneous studies of the postlarval stages. Womersley, in a taxonomic compendium, has described and redescribed some 230 species from the Asiatic-Pacific area. He has also made an outstanding contribution to the study of the postlarval stages of trombiculids from the world, but this is a pioneer work and the study of this subject is still relatively undeveloped: only 56 out of some 520 species of larvae have been correlated with the nymphs or adults. Fuller has made a meticulous study of type material in Holland and has added opinions gained from his considerable experience. A number of other workers—such as those involved in the Kansas Chigger Project—are engaged in intensive work on trombiculids and they will certainly be making considerable taxonomic contributions.

A large amount of material from Malaya—over 30 new species with 20 nymphs—has been studied but not described, and unpublished bionomic data have accumulated. In addition, over 15 undescribed species and 13 undescribed nymphs have been collected in North Borneo (by joint research teams in collaboration with Traub and with the financial support of the Surgeon-General's Office, Washington, U.S.A.), and in Sarawak (in collaboration with Tom Harrisson of the Sarawak Museum). It is very unfortunate that some of the more important material came to light too late to be made available to the above authors. It will be several years before the new material can even be described. Although discussion of much of the superficially studied material is premature, the writer believes that at this stage a useful and worth-while appendix can be given to the three monographs already published, so that workers may draw upon some of the Malaysian material in interpreting them and perhaps in dealing with their own taxonomic problems. The writer is aware that he is laying himself open to heavy criticism for some of the prematurely published opinions; nevertheless, the sound council of withholding opinions until they mature may be better for one's reputation but in this particular case it would not be helpful. The taxonomy of the trombiculids is still unsettled even at subfamilial and generic levels, and it must be made clear that the object of this paper is to offer data and a few tentative opinions based on the Malaysian material so that fellow-workers can use them as they see fit in clarifying the taxonomy of these mites. It offers four things: comments on the taxonomic significance of certain characters; some bionomic information of taxonomic interest; provisional revised definitions of genera and subgenera given in the light of the material studied in Malaya over the last five years; and lists of Old World species more or less up to date (early 1953). In order to make the publication more compact and the text easier to scan, authors have been omitted except where there might be confusion, and the trivial names are freely used without their generic initial; the species concerned are those listed by Wharton & Fuller followed by Womersley (who added many new species).

THE TAXONOMIC IMPORTANCE OF VARIOUS CHARACTERS

The various genera and subgenera have apparently been raised in three different ways. Firstly, a genus may be raised on a useful key-character, by which we mean characters, such as the presence of teeth on chelicers, which are convenient for the construction of artificial keys; but these genera have a habit of becoming more and more painfully artificial and sometimes also of accumulating species which are not congeneric—this most commonly happens because it is difficult for the taxonomist not to come to look upon specimens as chitinous patterns on slides, rather than as living creatures. An example is the genus *Schöngastia* (p. 150).

Secondly, a monotypic genus may be raised to accommodate a species with outstanding characters. If it does not remain monotypic, then it is often found that the genotype is not

typical of the whole congeneric group, having in fact drawn attention to itself by some excessively developed character or other. The genus *Doloisia* (p. 157) and subgenus *Trombiculindus* (p. 141) are examples. It has often happened in the Trombiculidae that the characters chosen for generic separation are recurrent polyphyletic characters, which appear independently in various unrelated groups. Such characters and their significance are discussed below. In the case of such genera raised on outstanding characters or groups of characters, it may later be found that a series of the other species puts the genotype in its proper perspective and the genus may then be identified through that series with some other genus, or it may appear to be at the most of no more than subgeneric rank. The selection of some exceptional species as the type of a new genus may give rise to a long delay before genuinely congeneric species are accommodated: the result in any case is frequently a genus of which the genotype is actually not typical of the natural group. This may not be very important, but the delay in recognising the congeneric species may be important and it is simply necessary to bear this in mind constantly. It follows, therefore, that monotypic genera should be raised cautiously and for exceptionally good reasons, especially in the earlier stages of classification.

The third way in which a genus or subgenus comes to be recognised is as a distinct species-group which is in time considered to have a higher status. An example is the *tsutsugamushi*-group of Nagayo and his colleagues. This group was recognised early because a number of similar species were found together in Japan, and the genus *Leptotrombidium* was proposed to accommodate them. This genus is temporarily considered as a subgenus of *Trombicula* sensu lato. Brennan (1952) has drawn attention to the *T. cynos* group as a potential genus. In the case of such genera, a good representative genotype can be selected from the group. This is important because the only question one may ask of a new species is whether or not it is congeneric with any known genotype.

A review of the progress of trombiculid taxonomy reveals four important stumbling blocks, viz. (a) incomplete early descriptions, making many comparisons impossible without reference to the genotype itself—this should be remedied by the redescription of type material (*vide* Fuller 1952) and by the publication of detailed and illustrated comparisons with related species at every opportunity. (b) The interpretation of recurrent polyphyletic characters. (c) The delayed study of the postlarval stages and the interpretation of post-larval characters. (d) The inadequate genotype of *Trombicula*—it is proposed in this paper to adopt, as a provisional substitute for the genotype, a species known in both larva and nymph which appears for very good reasons to be very close indeed to it, if not identical. It will thus at least be possible to build up a consistent subgenus. Points (b) and (c) are discussed below.

Interpretation of recurrent polyphyletic characters

A number of characters are now well recognised as being of polyphyletic origin and occurring as the same deviations from the standard in different groups. There should be a tendency to acknowledge and erect subgenera rather than genera when such characters are themselves made the chief points of difference. Care should also be taken to avoid grouping unrelated species because they share such a recurrent character. Furthermore, only a long study of adequate numbers of species may show whether a recurrent character should be considered as of more than specific importance. It may be wise in each case to start by ignoring the recurrent character completely and attempting to discover the relationships of the species concerned on the remaining characters. Audy (1952) has commented on the poor chitinisation and the posterolateral peninsulas of the scutum of *Trombicula dimolinae*: this group might include members in which the occurrence of PL setae off the scutum is no more than a specific character. In a group related to *Doloisia* (p. 157) this same character appears perhaps to be of subgeneric importance. The more important recurrent polyphyletic

characters are listed below together with references to pages where they are discussed or illustrated.

1. *Variation in the extension of the scutum* to exclude or include setae.—A reduction of the scutum, leaving the PL setae isolated, is encountered in *Tecomatlana*, *Trisetica*, and *Sauriscus* (of which *Sauriscus* at least, and perhaps *Trisetica*, may not be congeneric with *Tecomatlana*; p. 149). *Anomalaspis*; *Speleocola*(?); *Ascoschöngastia* (p. 155), *Pseudoschöngastia* (p. 155); *Apolonia*, *Womersia* (p. 165). This character is discussed by Womersley (1953, this *Study* p. 120). Extension of the scutum to include some of the dorsal setae is especially developed in the Gahrlepiinae (Walchiinae), but it is also encountered in the following, either with inclusion of dorsal setae or reduplication of the PLs: *Novotrombicula* (p. 149), *Heaslipia* (p. 149), and *Mackerrasiella* Wom. 1953: (p. 114)

2. *Scutal submergence and cuticular encroachment*.—A number of unrelated species show some encroachment of the cuticle onto the scutum, or even a partial submergence of the scutum, e.g. *Eusch. rectangulare* (Womersley 1952:186), *T. dimolinae* Audy 1952:139, and *Speleocola tardaridae* Lipovsky 1952:132. The submergence of the scutum is more complete and regular, and in several species apparently of a different nature, in the heterogeneous genus *Neoschöngastia*, and this requires further investigation (see comments, pp. 133, 156).

3. *Division of the femora of legs II and III*.—This has been accepted by many authorities as the chief character which distinguishes the Gahrlepiinae from the Trombiculinae. The division of the femur is a false articulation, sometimes evident only on the ventral aspect of the femur, and in some species (*Pseudoschöngastia*) the division may be difficult to detect in one or other of the legs—although as Brennan (1952) has pointed out, there is no doubt about the division on careful examination.

A species of great taxonomic interest in this connexion is *Schöngastia oudemansi*, the larva of which is distinctive and clearly not congeneric with the other species of *Schöngastia* s. str. (p. 150). It should therefore be taken out and either accommodated in *Euschöngastia* s. lat. or given a new genus or subgenus, the genus or subgenus *Schöngastia* s. str. being redefined accordingly. Fuller (1952) has, we think rightly, placed this species in new genus, *Walchiella*, which however automatically falls in the Gahrlepiinae as at present defined. Both *Walchiella* and the genus *Pseudoschöngastia* have therefore been placed in the Gahrlepiinae by Wharton & Fuller (1952). But the Gahrlepiines form a notably consistent group in both larval and postlarval stages, while *oudemansi* is a typical Trombiculine in all larval and postlarval characters except the division of the femora in the larva. Furthermore, some 21 species, of which 2 are described in this *Study* (p. 84), have now been found which show characters intimately relating *oudemansi* to similar forms without cheliceral teeth but with divided femora, and to others with undivided femora, including *E. lacunosa* (Gater). The nymphs of 4 of these forms are available and they share so many characters with the Trombiculinae and differ on so many diagnostic points from the twelve described gahrlepiinae nymphs, that the affinities of the *oudemansi*-group would appear to lie with the Trombiculinae and near to the *lacunosa*-group. For this reason, we here treat *Walchiella* as a subgenus of *Euschöngastia*, probably related to the sister *lacunosa*-group.

The only reason for suspecting that the *oudemansi*-group is intermediate, linking the Trombiculinae with the Gahrlepiinae, lies in the division of the femora, and *oudemansi* in fact fits more uncomfortably into the Gahrlepiinae on general characters than it ever did in the genus *Schöngastia* s. str. from which it has rightly been rescued. The division of the femora appear to have been independently acquired. Once this character in the legs is not given prime subfamilial importance, the genus *Pseudoschöngastia* also can be seen as being more properly trombiculine; but this genus is different from the *oudemansi*-group in general characters

so that it might in fact be found to represent a link with the Gahrlepiinae; nevertheless, it would appear that the proper place for this genus is at present also with the Trombiculinae. It would almost certainly be a mistake to raise a subfamily for these mites, at least at this stage, because it would be based on the division of the femora, a character of uncertain importance which has probably been independently acquired by *Pseudoschöngastia* and the *oudemansi*-group so that there would arise a simultaneous demand for raising a second subfamily, which is certainly premature. Recent studies of the *oudemansi*- and *lacunosa*-groups have thus greatly strengthened the views expressed by Womersley (1952:12).

4. *Modification of setae*.—This is discussed under *Trombiculindus* (p. 141) and *Fonsecia* (p. 148). Foliate expansions of setae are found in *Trombiculindus* (p. 141), the *Eusch. foliata* group (p. 154), and some *Acomatacarus*. Peg-like modifications or basal swelling of the setae may be noted in *Fonsecia* (p. 148), the dorsal setae of *Eusch. causicola*, the coxal seta on *Trombicula consueta*, and in several leeuwenhoekiiines (*Nothotrombicula*; *Audyana*!). The setal bases of body setae are generally well-chitinised and conspicuous in species of *Walchiella* and the *Eusch. lacunosa* group (p. 153), and in the former subgenus they are further developed into platelets [in *E. (W.) heaslipi*, *traubi*]. Such platelets are also encountered caudally in *Neoschöngastia* species (*entomyza*, *owiensis*, *retrocincta*, *yeomansi*), and in a different form in *Guntherana*. Anal plates are present in two species of *Schöngastiella* (*arona*, *birella*) described by Traub & Evans, 1953:95.

The post-larval stages

1. *Diversity of larval/post-larval stages*.—Most species of trombiculids are known from the larvae, but the number of known nymphs and adults is rapidly multiplying. There appears to be very much less specific and generic variation in the non-parasitic post-larval stages than in the parasitic larval stage. For example, the nymphs of *Heaslipia gateri*, *Trombicula hastata*, and *T. consueta* are difficult to separate and appear to be closely related, but the larvae are very different. Similarly, the nymphs of *Gahrlepiea ornata* and *Walchia lewthwaitei* are closely alike. This may to some extent be because a number of taxonomic characters of importance in nymphs and adults still remain to be recognised. On the other hand there is evidence that there may sometimes be more obvious differences between nymphs than exists between the corresponding larvae, an example from Malaya being the confusion of *T. rara* with another species (to be described) from pill-millipedes until differences in the nymphs led to a re-examination of the larvae (corrigendum on p. 427 of Womersley 1952 refers). At least two other examples have been found (Womersley in correspondence), but the best published examples are those of American species of *Blankaartia* (= *Megatrombicula* Michener) and of *Trombicula autumnalis* in England. Michener (1946), in discussing *T. (Blankaartia) attenuata*, *alleei*, and *velascoi*, of which "not every larva can be definitely placed in one species or another," observed that the corresponding adult characters were conspicuously different. Richards (1950) described considerable variation (five forms) in larvae which were all considered to be *T. autumnalis*. Nymphs were reared only from one form of larva and they showed no particular variations. Womersley (1952:354, 365) considers that Richards was dealing with at least two species, *T. autumnalis* and *T. inopinatum*; but there were nevertheless 5 main forms. However, Jones (1952) has described two easily distinguished forms of nymph bred from a single form of larva of *autumnalis*.

It is of course well recognised, e.g., in the Diptera Culicidae, that rigid ideas on the employment of either larval or adult characteristics are to be deplored. Certainly, species and subgenera based entirely on morphological larval characters may be fully acceptable though the free extension of this to genera (and even to subfamilies, as has been done) is debatable in particular instances. The Culicidae offer a number of examples of specific differentiation in

one stage of the life-cycle but differently, or hardly at all, in the other: in an example from the *Anopheles umbrosus* group, Reid (1950:315) has remarked that it "looks as if the evolution of larval and adult characters in some of these species has proceeded independently along somewhat divergent lines." This is to be expected when the larval and post-larval stages lead such very different lives. Adaptive and other modifications involving the larvae cannot be expected to be reflected by corresponding modifications in the post-larval stages, and *vice versa*. Our main interest in trombiculid mites at present is in their behaviour as parasitic larvae, and it would probably be rational to give more weight to a larval system of classification whenever this is seriously at variance with a post-larval system. Compromises may readily lead to serious difficulties. There is no doubt that taxonomic revisions of the trombiculids should be made very cautiously and not be based on local studies, at this stage, however meticulous these may be.

2. *Standard measurements of Nymphs/Adults*.—The use of the following measurements in the descriptions of nymphs and adults has been agreed upon jointly by Dr. Douglas Gould and the present writer, based on the work done by Jenkins (1949), Wharton *et al.* (1951), Womersley (1952, and various papers), and Wharton & Fuller (1952). The measurements and their abbreviations are offered provisionally pending the publication of joint papers in the next *Study* in this series. The suggestions made below will doubtless be elaborated during the completion of these papers. In describing nymphs and adults the worker confronted by a badly mounted or faded specimen must be borne constantly in mind. Points from which measurements are made should be clearly discernible (e.g., the exact ends of the crista cannot be accurately decided especially in old specimens, hence its length will vary greatly when measured by different workers). Ratios are generally of much greater value than arrays of measurements. A method of graphic or tabular presentation (as with Standard Measurements of larvae) is being devised, and the abbreviations are proposed with this in mind.

Suggested Standard Measurements (Fig. 1)—

Body : Length and Width of propodosoma.

Gnathosome: Lengths of femoral and tibial setae

Lengths of Claw and Tibia (ratio claw/tibia)

Length of cheliceral blade

?Relative proportions of palpal segments.

Scutum: Cristo-rectal length (CTL) from where crista expands into saddle to first median tectal setal base.

ASL—anterior scutal length

SB—sensillary bases

Ratio ASL/SB

C—crista

K—length of carina, when present

PSL—posterior scutal distance

PAD—posterior apodeme

E/ED—diameter of eye/interocular distance

TS—tectal (epistomal) seta(e)

SS—parascutal setae

SENS—sensilla

Legs: proportional lengths entire legs when possible

Length/Height, Tarsus I (and L/Width, as height may not be measurable in many)

Lengths, Tarsus I/Tibia I

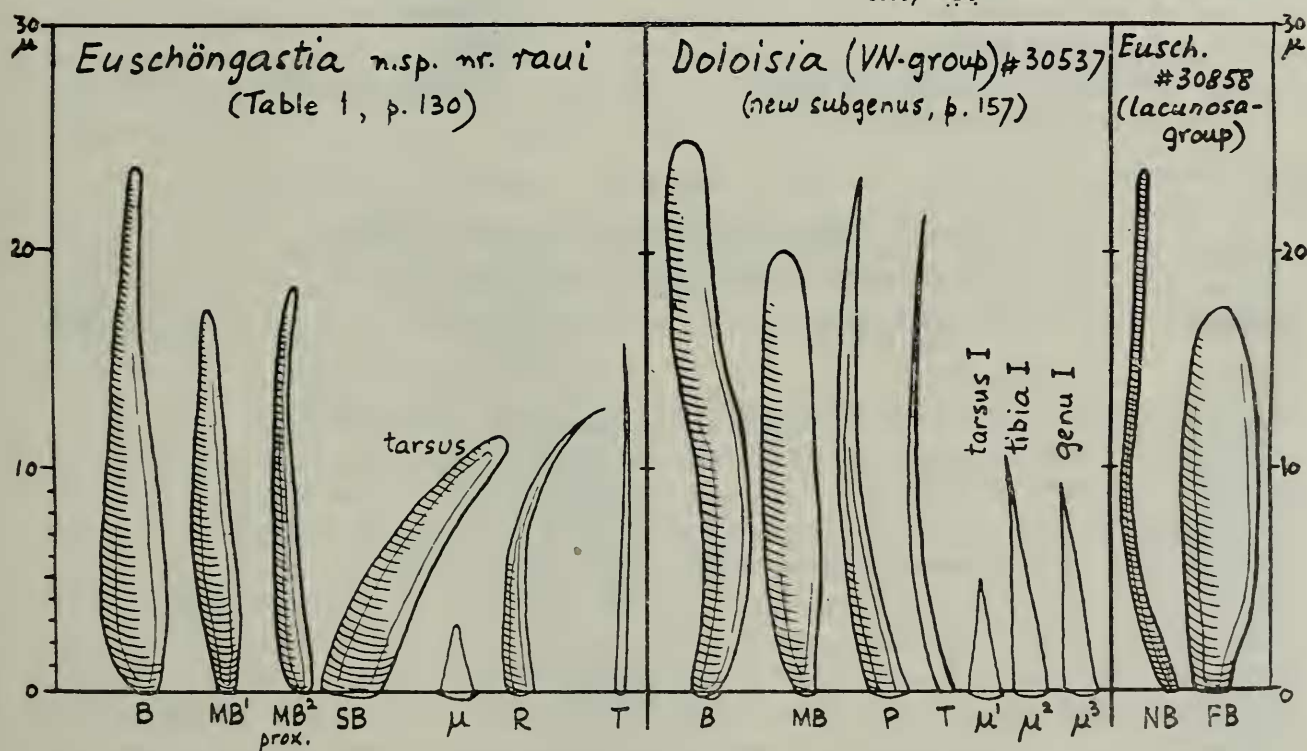
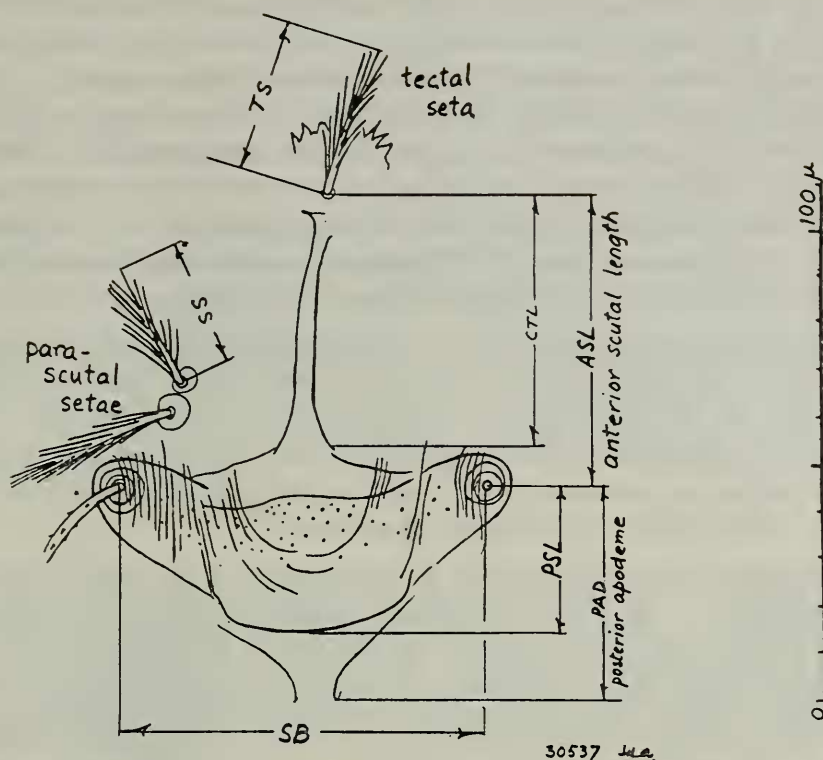
Lengths, Tarsus II/Tibia II

Genitalia: ?Ratio of axial lengths anterior and posterior suckers in nymphs

Ratio of axial lengths genitalia to anus.

Body Setae: lengths and wherever possible ratios of lengths of anterior dorsal setae, posterior dorsal setae, and ventral setae.

3. *Chaetotaxy of legs, Nymphs/Adults*.—The leg setae have been almost completely ignored because they rapidly become difficult to study in old mounts and because they occur in dense setal forests which would deter the most enthusiastic worker. It is however necessary to explore these setae for their possible taxonomic importance, and the present writer has found that the forests of setae can be reduced to some sort of order without undue effort.



1. Scutal measurements and leg chaetotaxy of Nymphs and Adults.

The scutum, of a Nymph of *Doloisia* (VN-group, new subgenus) sp. "VN", shows the more important new measurements and their abbreviations, as listed on page 128.

The sensory setae only (omitting the ordinary barbed or plumose setae which should in practice be drawn with the others) are shown for the legs of the nymphs of *Euschöngastia* sp. nr. *rauli* and *Doloisia* (VN-group) sp. "VN"; and in addition, two of the setae (NB, narrow; and FB, flask-shaped) from the nymph of an undescribed species in the *E. lacunosa* group.

Note: This and the following illustrations (pp. 139, 158), with the exception of fig. 3D, are experimental, being reproduced from pencil sketches on thin typing paper, converted to black-and-white line drawings photographically by a technique which is being described elsewhere.

The major types of seta are first picked out, measured, and sketched as shown in Fig. 1. These setae are generally of the following types: (a) Ordinary barbed or pectinate setae (the others presumably being specialised sensory setae of various sorts). (b) Blunt striated setae ("B"), which are typical solenidia and similar to the tarsal spurs of the larvae. (c) Pointed striated setae ("P"), similar to the pointed tibialae and genualae of larvae, and obviously of the same type as the blunt setae. (d) Tapering setae ("T"), slender and usually obviously distinct from the pointed solenidia; these setae appear not to be striated but this requires closer study. (e) Recurved setae ("R"), relatively short, sharp-pointed, and recurved towards the proximal part of the leg; apparently striated. (f) Microsetae ("μ").

One or more distinct representatives of each of these types may be found in a given species, and may be given designations, e.g., LB, MB, FB for long, medium-length, and thick flask-shaped solenidia, or BN for a narrow cylindrical one. The species of nymphs which have so far been examined usually have 6 to 10 distinct setae. As we have already noted, it is important that these be sought out, measured, sketched to scale, and given some sort of letter-designation at the outset. This takes a surprisingly short time.

The next stage is the enumeration and tabulation of the setae, type by type and segment by segment (Table I). It needs very little practice for this to be done quickly. Individual workers will prefer their own systems, but the writer has now come to prefer tabulating the pointed (P, R, μ), blunt (B), and tapering (T) setae in three columns, using the following small letters to suggest roughly the main distribution of the setae on the segment concerned:

d, dorsal aspect.	p, proximal.
v, ventral aspect.	s, distal.
l, lateral (or posterior) aspect.	t, terminal, e.g., near tarsal claw.
m, medial (or anterior) aspect.	

TABLE I.

Example of tabulation of setae on legs of a nymph,
Euschöngastia species in MS, *raui*-group (Fig. 1).

Segment.	Pointed strong setae (P).	Blunt fingerlike setae (B).	Fine tapering setae (T).
Tarsus I	μ (mid-dorsal) ... 11 t (4tm, 4tl in vertical rows)...	10 (8d, m.l.) ... 9M (8s, lp, more slender proximally) ...	—
Tibia I	60Rv (approx. in 9 rows) ... μtl. 2Rt (d.m) ...	2-3S (l.lv) ... 22 (distal 2/3, dt) ...	—
Genu I...	μst ...	3 (2l, tm) ...	16 (prox 2/3; 6d)
Telofemur I	t ...	—	20s
Tarsus II	RtI (terminala) μs (prox. to MB)	M(t) S(p) (not thick)...	—
Tibia II	—	SNt ...	1-2 (p.s)
Genu II	—	—	3s (1pd)
Telofemur II	(t)	—	—
Tarsus III	—	M (st; 15μ) ...	s (prox. to MB)
Tibia III	—	MNtm ...	5 (dt, 2d, 2ps)
Genu III	—	—	2d (tandem)
Telofemur III	t	—	—
Tarsus IV	Rtl	M (prox to LT)	2 (p, & t to MB)
Tibia IV	Rt	—	7 (5p in group)
Genu IV	—	—	5 (4s, p)
Telofemur IV	—	—	—

A meticulous study of the leg chaetotaxy is necessary. This would best be made as a comparative study with the Trombidiidae and related prostigmatic mites. The development of the specialised setae from nymphal to adult stages of the Trombiculidae is also of great interest. The excellent studies made by Grandjean (1943, 1947) may be taken as a model.

4. *The structure of the scutum (crista), Nymphs/Adults.*—There appears to be no satisfactory account of the detailed structure of the scutum, and artists drawing these structures have sometimes shown only one plane, so that similar scuta may be given very different appearances by different artists. The artist himself is seriously handicapped by the lack of a comparative study of this structure. The present writer suspects that there are some fundamental differences in the structure of the scuta of certain groups of trombiculids. A comparative study of uncrushed material as well as serial sections is likely to yield some valuable taxonomic clues. The features which will most repay investigation appear to be (a) the structure of the chitinous vault or roof (*areola*) of the *area sensiliger*a, between the sensillary bases, (b) the development and structure of the apodeme beneath the scutum, (c) the shape of the space enclosed by the walls of the apodeme beneath the *area sensiliger*a (this space may extend towards the chitinous column of the *crista*), and (d) the development of the scutal structures from nymph to adult. The eyes, the para-scutal setae, and the tectum with its seta(e) should be studied together with the scutum.

The larval stage*

1. *Standard Measurements.*—A comparison of standard measurements of the scuta can be misleading and the ready separation of different populations of chiggers by statistical analysis of their measurements is a new pitfall for the unwary. Ratios are generally more valuable than linear measurements. Superimposing tracings of scuta, drawn to the same scale, is a useful way of deciding which ratios are likely to help in separating particular species. Ratios between scutal measurements and measurements of other chitinised parts may be particularly valuable. The present writer has been measuring the tarsus-plus-pretarsus for other reasons and would prefer to take scutal/tarsal ratios. Traub has shown that a scutal/coxa ratio (PW: coxa II) is of great value in separating *T. akamushi* from *T. deliensis* (Traub & Audy, 1953: 86).

Jadin & Vercammen-Grandjean (1952) have added to Womersley's standard scutal measurements but the writer has no comment to make on these except to plead that the number of measurements should be cut down to the absolute minimum. Only usage and experience will allow us to decide what the minimum should be. Certain measurements are useful in some groups but not in others; a routine tabulation will therefore encourage either superfluous measurements or unfortunate omissions.

2. *Chaetotaxy.*—Wharton (1948) found that a detailed study of the chaetotaxy of the legs was of assistance in the recognition and classification of trombiculid larvae, and the importance of this finding has been conclusively demonstrated since. Brennan & Wharton (1950) have surveyed the subgenus *Neotrombicula* in North America and have shown that the leg setae are of specific importance and can be used to advantage in constructing keys. More recently, Brennan (1952) has done the same with the four known American members of the *T. cynos* species-group, while Audy (1952) has dealt with a mixed collection of species of *Trombicula* from bats in Malaya. During the course of studies of Malayan material, in which comparisons have been made with the observations of Wharton and of Brennan, some ideas have emerged concerning the importance of various details, and these are noted below.

* Since this paper went to press, P. H. Vercammen-Grandjean, of the Laboratoire Medical, Province of Kivu, Bukavu, Belgian Congo, has made a most useful observation of a taxonomic character which has hitherto escaped attention, namely, the nature of the internal annular chitinous thickenings of tarsi I in the larvae. These may be partially or fully developed, and there may be one (proximal) or two (proximal and distal). A detailed assessment of this character is being made the subject of a joint paper by Vercammen-Grandjean and Audy, but we may here note that the second distal thickening appears to be regularly present in the Gahrlepiines, in the species of *Walchiella* and the *lacunosa*-group so far examined; while it is poorly developed in some members of the *indica*-group. It is present in a few members of the subgenus *Trombicula*, and is clearly shown in Lipovsky's drawings of *Speleocola*. It is however absent in most chiggers.

The sensory rods (solenidia) of tarsi I and II have been named spurs by Wharton, but Womersley has objected to this use of a term which has special meaning in entomology. Furthermore, the stout blunt character which distinguishes the tarsal spurs may also be shared by the distal tibiala. It is suggested therefore that the sensory rods of the tarsi may be called tarsalae, and the microspurs microtarsalae, thus bringing the nomenclature into line with that of the corresponding setae on the other segments.

Some species or groups tend to have heavily barbed leg-setae, among which nude setae are particularly significant. Other species or groups, e.g. the *indica*-group (p. 154), have leg-setae on which barbs are generally poorly developed: the presence of nude setae among these is usually of much less significance, and these setae should not be freely compared with similar nude setae in other groups. The presence of ordinary leg-setae of different lengths, i.e. long setae and short setae, is however of taxonomic importance, not only at the subgeneric level (as with *Neotrombicula*, p. 143) but at the specific level (the long nude or almost nude setae of *Eusch. audyi*, for example). A third point about these ordinary leg setae also concerns all the setae of the body and palps, and that is that there is no full agreement among acarologists on the proper description of the various types of barbs or other processes which clothe these setae. Descriptions such as *branched*, *barbed*, *plumose*, *ciliated*, *pectinate*, *trifid*, are not used with the same meanings by different workers. The exact description of the setae on body, palps, and legs is however of considerable taxonomic importance and it is proposed in a later paper to illustrate and describe terms which have been agreed upon by those taxonomists concerned.

Apart from inter-specific differences, various combinations of characters, especially in the setation of leg III, have distinct subgeneric and even generic importance. The lengths of the tarsi (including the pretarsus and the bases of the claws so that measurements can be made accurately) and of the sensory rods (tarsalae, spurs) on the tarsi are being recorded for the Malaysian material for later assessment but it is not yet known if this is worth while. The following characters are recorded roughly in the order of what appears to be their importance.

All legs: lengths in relation to thickness (as it is both tedious and inaccurate to attempt to measure legs which are considerably bent, the tarsi might perhaps be taken to represent the legs); plumosity or nudity, and relative lengths, of the leg setae generally; occasionally, claws and empodium deserve comment.

Leg III: all specialised setae, especially the whip-like setae. The latter appear to be of two distinct kinds: true solenidia, like the femoralae and genualae, which are unusually long and whip-like, generally curved, showing the hollow refractile appearance and often the striae of the shorter setae; and long nude setae which resemble the ordinary non-specialised setae. The latter are usually straight and outstanding, so that the description whip-like is not very apt; similar setae may carry traces of ciliations or barbs near the base, others may carry a few barbs but have a long free tip (cf. *T. flagellifera*, *tuhana*). The terms mastitarsala, mastitibiala, etc. are retained for the latter type of seta, while the former type is described as whip-like tibialae, genualae, etc. (Audy, 1952): Wharton, in correspondence, states that this is the correct usage of his terms, while he also refers to the short (not whip-like) nude setae as, e.g., "a short mastitibiala".

Leg I: The position of the microtarsala in relation to the base of the tarsala; the general shape and size of the sensory setae (these may be short, stout, slender, long, pointed or blunt; the distal tibiala on leg I or II may be blunt while the proximal seta is pointed and more slender). The relative lengths of the microsetae (the microtibiala and microgenuala may at times be very long); in addition, the microsetae may occasionally be modified, as in the hook-like microtarsala of *T. harrisoni*. Occasionally the presence of long nude, plumose, or pectinate setae, sometimes mastisetae, on the femur; occasionally, the length of the parasubterminala relative to the subterminala.

Leg II: position of microtarsala relative to base of tarsala; whether the tibialae are in tandem or not.

In general, an attempt has been made in all descriptions to refer measurements to comparisons with other features which will be before the observer on the same part of the specimen, so that setae may be compared with the lengths of segments, or, for example, the microsetae or parasubterminala with their associated sensory setae. In illustrating the leg setae, it is probably best to concentrate effort on the shapes and positions of the sensory setae, and to show only the bases of the other setae together with a few examples to illustrate the type

of branching. It is necessary to show at least all the bases of setae in order to help the worker confronted with a specimen in which setae may be missing.

Certain features are so regularly present that nothing whatever is gained by their enumeration in every description. The five special setae on tarsus I are an example. Only the rare deviation from this need be noted, as in the case of the multiple spurs in *Phrynacarus*.

Regarding the body setae, Audy (1952:153) has appealed for a standardisation in the description of the dorsal (DS), caudal or postanal (CS) and ventral (VS) setae. The following is an example of a standard description suggested by him: "*Body setae*: DS fairly slender, similar to PL scutal setae, with short barbs, arranged in rows but with irregular setae medially and laterally in the first row and laterally in other rows, e.g., 2.4.10.4.12.6.6.4, totalling 44-60 DS (42 to 32 μ ; humeral setae 45 μ) + caudal setae (CS) in rows on level of and behind anus, 14-16 CS (total setae of dorsal type 64-74) + 22-26 VS (27 μ) more slender, with two or three lateral barbs and a free pointed tip, arranged roughly in rows and more or less distinct from the caudal setae. One pair of sternal setae between coxae I and two pairs of sternal setae between coxae III." Reasons for attention to these differences are given under the genus *Fonsecia* below (p. 148).

3. *Convergence in larval characters*.—The very close resemblance between *Trombicula munda* and *Euschöngastia indica*, mentioned on p. 154, is one example of a troublesome problem for the taxonomist. The occurrence of *T. munda* on particular hosts in company with large numbers of *E. indica* and *E. audyi*, e.g. on *Rattus r. diardii* in houses, may be interpreted by assuming that its life-cycle is passed mostly in or near the nests of its hosts. The resemblance between *munda* and *indica* would appear to be due to a convergence of characters, and in this particular instance this convergence might possibly be associated with the similar habitats which the two species appear to share. The present writer is reluctant to assume that there need be any particular taxonomic relationship between these two species in spite of the morphological evidence. It is obvious that the nymph of *munda* is of exceptional taxonomic interest, but efforts to obtain it have so far failed because this is an uncommon species.

Another example of convergence is to be found in *T. beltrani* Hoffman (from a bat in Mexico), of which the scutum, the curved claws, and the peculiar small angulated (but not toothed) chelicers, give the larva a curiously close resemblance to members of *Doloiisia* sensu lato, from ground-mammals in Malaysia and Africa. Both these examples of convergence are incidentally between the *indica*- and *Doloiisia*-groups, which have many features in common (p. 154), and what we take to be the subgenus *Trombicula*.

When the genus *Neoschöngastia* (see p. 155) is studied intensively it will be necessary to consider to what extent the characteristic submergence of the scutum is or is not a polyphyletic character, associated perhaps with the avian habitats, possibly resulting in a convergence of characters in larvae which should in fact be accommodated in several genera.

4. *Complexes of "seasonal" forms*.—The presence in the same country of a number of closely related species which differ not only morphologically but in having different seasonal incidences is extremely interesting. Examples are species of *Leptotrombidium* in Japan (Nagayo *et al.* 1927), of *Neotrombicula* in North America (Brennan and Wharton, 1950) and the forms of *T. (Neotrombicula) autumnalis* in Britain (Richards, 1949). There is a possibility here of a form of ecological subspeciation which is worth investigation.

For example, the species of *Leptotrombidium* (*akamushi*-group) studied by Nagayo *et al.* in north-west Honshu, Japan, showed different seasonal incidences. *T. akamushi* was the dominant species in mid-summer (a single peak of 21 mites per vole was recorded for August, 1919, dropping to a negligible number in October). *T. intermedia* appeared for only three

months with a peak in October. *T. pallida* showed one peak in May-June and another in September-October (which might suggest that this is a cold-weather species with a 3-4 month summer cycle which is extended over some 8 months through the winter). *T. palpalis* resembled *T. pallida* in having two peaks but it appears to be a true winter species with a peak in November followed by a second between January and April, the summer trough being very low. A fifth species, *T. scutellaris*, was not studied by these authors, but it appears to have a single peak roughly coinciding with that of *T. intermedia*.

The five members of the *T. akamushi* group thus show different patterns of larval incidence, *T. akamushi* alone dominating the mid-summer. An important point is that though all these mites may infest the same hosts, this seasonal behaviour tends to isolate the populations of the different species by the phase-dislocation of their various activities. An interesting speculation presents itself. The overall climate in a country is broken up by features such as aspect, exposure, drainage, and local cloud-formation into a mosaic of local climates—so that for example, spring and autumn do not develop exactly in step on the north and south slopes of a mountain nor does a prevailing condition produce the same effect in a valley as it does on an exposed slope. Such local vagaries of climate, coupled with edaphic factors and perhaps phases of behaviour of the hosts, may therefore conceivably tend to set several populations of the same species out of step with each other in their life-cycle rhythms, in which case a degree of isolation of the populations should tend to develop. The original "seasonal" species may thus in effect be broken up into a number of isolated populations exposed to different selective influences. The writer is not in a position to suggest that something of this sort may explain the presence of some of the forms of *Leptotrombidium* in Japan or of *Neotrombicula* in America and Britain, but such a possibility should be borne in mind when considering the peculiarities of speciation in closely similar forms with seasonal individuality.

PROVISIONAL DEFINITION OF TAXONOMIC UNITS OF OLD-WORLD CHIGGERS

The following list shows the families, subfamilies, genera, and subgenera as accepted by Womersley (1952), and Wharton and Fuller (1952), and as tentatively accepted in the present paper:

SUBFAMILIES, GENERA, AND SUBGENERA

Abbreviations:	<i>n, a.</i> :	nymphs, adults known
	<i>N, A.</i> :	known only from nymphs, adults (larvae unknown)
	<i>OW.</i> :	genus/subgenus known only from Old World
	<i>NW.</i> :	genus/subgenus known only from New World
	*	genus/subgenus described since the publication concerned

Present paper.	Wharton and Fuller, 1952.	Womersley, 1952.
TROMBICULIDAE ?s. s.	TROMBICULIDAE s.l.	TROMBICULIDAE s.s.
TROMBICULINAE	TROMBICULINAE	TROMBICULINAE
Group A:		
<i>Trombicula</i>	<i>Trombicula</i>	<i>Trombicula</i>
(<i>Trombicula</i> s.s.) ?OW. n.a. ...	(<i>Trombicula</i> s.l.+) ...	(<i>Trombicula</i> s.s., partim)
(<i>Eutrombicula</i> s.s.) n.a. ...	(<i>Eutrombicula</i>) ...	(<i>Trombicula</i> , partim)
(<i>Leptotrombidium</i> s.l.) n.a. ...	(<i>Leptotrombidium</i> s.s.) ...	(<i>Leptotrombidium</i> s.l.)
(<i>Trombiculindus</i> s.l.) OW. n. ...	(<i>Trombiculindus</i> s.s.) ...	(<i>Trombiculindus</i> s.s.)
(<i>Crotiscella</i>) NW.	(<i>Crotiscella</i>)	(<i>Crotiscus</i>)
(<i>Neotrombicula</i> s.s.) n.a. ...	(<i>Neotrombicula</i> s.s.) ...	(<i>Neotrombicula</i> s.l.+)
(<i>Blankaartia</i> s.s.) n.a. ...	(<i>Blankaartia</i> s.s.) ...	<i>Tragardhula</i> (<i>Blankaartia</i> s.l.)
<i>Fonsecia</i>	(<i>Fonsecia</i>)	<i>Trombicula</i> (<i>Fonsecia</i>)
<i>Tecomatlana</i>	<i>Tecomatlana</i>	<i>Tecomatlana</i>
(<i>Tecomatlana</i>) NW.	= <i>Sauriscus</i> = <i>Trisetica</i>	= <i>Sauriscus</i> = <i>Trisetica</i>
(<i>Sauriscus</i>) OW.		
(<i>Trisetica</i>) OW.		

<i>Speleocola</i> NW. n.	*	*
<i>Anomalaspis</i> NW.	*	*
<i>Myotrombicula</i> OW.	<i>Myotrombicula</i>	<i>Myotrombicula</i>
<i>Heaslipia</i> OW. n.	<i>Heaslipia</i>	<i>Heaslipia</i>
<i>Novotrombicula</i> OW.	<i>Novotrombicula</i>	<i>Novotrombicula</i>
<i>Ipotrombicula</i> OW. A	*	<i>Ipotrombicula</i>
<i>Speotrombicula</i> NW. A.	<i>Speotrombicula</i>	<i>Speotrombicula</i>
Group B:						
<i>Oenoschöngastia</i> OW.	<i>Oenoschöngastia</i>	<i>Oenoschöngastia</i>
<i>Radfordiana</i> OW.	*	<i>Radfordiana</i>
—	—	—	—	—	—	<i>Schöngastia</i> s.l.
<i>Schöngastia</i> s.s. OW. n.a.	<i>Schöngastia</i>	(<i>Schöngastia</i>)
<i>Euschöngastia</i> s.l.	<i>Euschöngastia</i> s.l.	(<i>Eusch.</i> = <i>Ascosch.</i> s.l.)
(<i>Euschöngastia</i> s.s.) NW.	—	—
(<i>Helenicula</i> nov.) OW. n.	—	—
(<i>Walchiella</i>) OW. n.a.	<i>Walchiella</i> in WALCHIINAE	(<i>Schöngastia</i>)
(?n. subg. <i>lacunosa</i> -group) OW. n.	<i>Euschöngastia</i>	(<i>Eusch.</i>)
(?n. subg. <i>indica</i> -group) OW. n.a.	<i>Euschöngastia</i>	—
<i>Ascoschöngastia</i> s.s. n.	<i>Ascoschöngastia</i> s.s.	—
<i>Pseudoschöngastia</i> NW.	<i>Pseudoschöngastia</i> in WALCHIINAE	—
<i>Neoschöngastia</i> n.	<i>Neoschöngastia</i>	<i>Neoschöngastia</i>
<i>Mackiena</i> OW.	<i>Mackiena</i>	<i>Mackiena</i>
<i>Guntherana</i> OW. ?a.	<i>Guntherana</i>	<i>Guntherana</i>
<i>Doloisia</i> s.l.	<i>Doloisia</i> s.s.	<i>Sch.</i> (<i>Eusch.</i>)
(<i>Doloisia</i> s.s.)	*	*
(n. subg. in MS) OW. n.
(?n. subg. <i>oculicola-crocidura</i> group) OW. n.	<i>Euschöngastia</i>	<i>Sch.</i> (<i>Eusch.</i>)
<i>Riedlinia</i> OW.	<i>Riedlinia</i>	<i>Riedlinia</i>
<i>Endotrombicula</i>	<i>Endotrombicula</i>	<i>Endotrombicula</i>
(<i>Endotrombicula</i>) NW.	(<i>Endotrombicula</i>)	(<i>Endotrombicula</i>)
(<i>Phrynacarus</i>) OW.	(<i>Phrynacarus</i>)	(<i>Phrynacarus</i>)
GAHRLIEPIINAE pro tem.						
			WALCHIINAE.		GAHRLIEPIINAE.	
<i>Gahrlepie</i> s.l.	—	<i>Gahrlepie</i> s.l.
(<i>Gahrlepie</i> s.s.) OW. n.a.	<i>Gahrlepie</i> s.s.	(<i>Gahrlepie</i> s.s.)
(? <i>Gateria</i>) OW. n.	<i>Gateria</i>	(<i>Gateria</i>)
(? <i>Giroudia</i>) OW. n.	*	*
(? <i>Schöngastiella</i>) OW. n.	<i>Schöngastiella</i>	(<i>Schöngastiella</i>)
(? <i>Walchia</i>) n.a.	<i>Walchia</i>	(<i>Walchia</i>)
<i>Eusch.</i> (W.) in TROMBICULINAE	<i>Walchiella</i>	<i>Sch.</i> (<i>Sch.</i>) in TROMBICULINAE
<i>Pseudosch.</i> in TROMBICULINAE	<i>Pseudoschöngastia</i>	<i>Sch.</i> (<i>Eusch.</i>) in TROMBICULINAE
(? LEEUWENHOEKIIDAE)	not recognised as a Family		LEEUEWENHOEKIIDAE	
LEEUEWENHOEKIINAE			LEEUEWENHOEKIINAE		LEEUEWENHOEKIINAE	
<i>Leeuwenhoekia</i>	<i>Leeuwenhoekia</i>	—
(<i>Leeuwenhoekia</i>) NW.	(<i>Leeuwenhoekia</i>)	—
(<i>Comatacarus</i>) NW.	(<i>Comatacarus</i>)	—
<i>Acomatacarus</i>	<i>Acomatacarus</i>	—
(<i>Acomatacarus</i>) n.a.	(<i>Acomatacarus</i>)	—
(<i>Austracarus</i>) OW.	(<i>Austracarus</i>)	—
(<i>Austrombicula</i>) OW.	(<i>Austrombicula</i>)	—
(<i>Hyracarus</i>) OW.	(<i>Hyracarus</i>)	—
(<i>Xenacarus</i>) NW.	(<i>Xenacarus</i>)	—
<i>Chatia</i> NW. n.	<i>Chatia</i>	—
<i>Shunsennia</i>	*	—
<i>Hannemania</i> n.a.	<i>Hannemania</i>	—
<i>Odontacarus</i> NW.	<i>Odontacarus</i>	—
<i>Whartonia</i> n.	<i>Whartonia</i>	—

APOLONIINAE s.l.			APOLONIINAE.			APOLONIINAE.		
<i>Apolonia</i> NW.	<i>Apolonia</i>	<i>Apolonia</i>		
<i>Sauracarella</i> OW.	<i>Sauracarella</i>	<i>Sauracarella</i>		
<i>Womersia</i> NW.	<i>Womersia</i>	<i>Womersia</i>		
? <i>Womersleyia</i> OW. n.	?? a TROMBIDIID			<i>Womersleyia</i>		
? <i>Grossia</i> OW.	*			<i>Grossia</i>		
? <i>Neotrombidium</i> a.	?? a TROMBIDIID			? <i>Neotrombidium</i>		
? <i>Nothotrombicula</i> OW.	?? a TROMBIDIID			<i>Nothotrombicula</i>		
? <i>Cockingsia</i> OW.	*			<i>Cockingsia</i>		
? <i>Mackerrasiella</i> OW.	*			<i>Mackerrasiella</i>		

The scheme of classification which follows is essentially provisional. Circumstances have precluded writing this preliminary account in collaboration. It has also been necessary to postpone publication of a paper (Audy, 1955) describing certain species of special taxonomic interest: this paper will be published in the following *Study* of this series, while only the essential references to it will be made here. In drawing up the present scheme, the diagnoses of the taxonomic units are generally those of Womersley and of Wharton & Fuller, with any existing anomalies between them resolved as far as possible, often by compromise. The origin of the diagnoses is acknowledged where necessary, with a note as to whether they are unchanged or have been modified; but the term "amended" is not used here as the writer believes it should be reserved for considered decisions and not provisional amendments. In making decisions as to the generic or subgeneric rank of a number of units the following tenets have been accepted: (a) valid genera and subgenera may be based on larval morphological characters alone; (b) biological features such as host-preferences or peculiar habitat-preferences should be included in the consideration of natural relationships and may guide one in according independent status to groups of species; and (c) special care should be exercised in dealing with recurrent polyphyletic characters. In defining these units, the principle has been adopted that at this stage it is advisable to expand them whenever this leads to a better organisation of the known species into the scheme of classification. In a few cases (e.g., *Schöngastia*) concepts of genera have however been restricted.

The Malaysian material comprises some 130 species of larvae and 73 nymphs, descriptions of a number of which are yet unpublished. This material has been scrutinised to see what light it can throw on the many taxonomic problems, but because a good deal remains to be studied carefully the opinions expressed are only tentative. They are nevertheless likely to be useful to other workers. The writer believes that the greatest need now is for all groups of two or more closely related species to be recognised and listed preparatory to detailed study; for exhaustive descriptions or redescriptions to be made of all genotypes and representatives of species-groups, so that proper standards are set for comparative studies and descriptions; for geographically local exhaustive studies of genera, subgenera, and species-groups to be made and to be followed by world-wide comparative studies; for the postlarval stages to be explored for more characters of taxonomic importance, and for more extensive breeding of these stages to be undertaken. These needs are guiding the work of this research team, particular importance being attached to the *akamushi*-, *wichmanni*-, *indica*-, *lacunosa*-, and *oudemansi*-groups, each of which includes a dominant species in Malaysia (although *T. wichmanni* is not dominant in our particular collections in Selangor, it is dominant elsewhere, and the group is represented in the Americas).

FAMILY TROMBICULIDAE EWING

Diagnosis.—(1) *Sensu stricto* after Womersley (1952:13, *verbatim*): Larvae with only 1 AM seta, or none, on scutum and no antero-median scutal process. Stigmata and tracheae absent (? rarely present). Nymphs and Adults figure-eight shaped, with a distinct medial constriction, and propodosoma not wider than hysterosoma. Crista anteriorly ending in a hyaline dentate epistome (tectum) furnished with a single ciliated seta. Eyes 1+1 or absent, when present either closely adjacent to sensillary area, or away from and in front of this area.

STUD. INST. MED. RES.

(2) *Sensu lato* after Wharton and Fuller (1952:40-41): there is nothing controversial in the broad diagnosis given by these authors, who unlike Womersley recognise only one family of chiggers.

Remarks.—Whether or not one accepts the single broad family or the two families Trombiculidae and Leeuwenhoekiidae, it is important to recognise that there are some relatively poorly studied “leeuwenhoekiid” groups of genera which appear to have a confusing number of affinities with the Trombidiidae. It may therefore help to add the following notes on the family Trombiculidae taken *sensu stricto*, so that comparisons may be made with the Leeuwenhoekiidae of Womersley (p. 163 below) and with the Trombidiidae (p. 166).

Larvae with a dorsal plate (scutum), very rarely with accessory dorsal plates (caudal in *Guntherana*; at bases of dorsal setae in a few species). Scutum posterior to gnathosome (apparently overlapping it only sometimes with extreme engorgement), without anterior median process or nasus (unless one is to include *Hannemania* on account of the constricted adults, see p. 164), usually with 5-6 scutal setae (2, 3 or rarely 4 setae anteriorly) but may be up to 20 (*Gateria* species); always with one pair of sensillae, filiform (rarely nude, usually barbed or plumose) or expanded. Eyes if present usually 2+2, often on a distinct ocular plate. Seta on fused palpal coxa posterior to base of palpal femur, usually with long barbs or branches. Femora of legs usually divided (7 segmented legs), sometimes (and regularly in Gahrlepiines) undivided in legs II and III. All coxae usually 1-setose; coxa I and/or II multisetose in typical *Dolosisia*, otherwise 1-setose; coxa III multisetose in several unrelated groups and frequently in the Gahrlepiines. Sternal setae 2 pairs, rarely 3. Larvae parasitic on vertebrates, very rarely on arthropods.

Nymphs and Adults mostly small (1 mm or less); body constricted (“figure eight”). Scutum with one pair of filamentous sensillae (sometimes spatulate or mid-shaft thickened) arising from a subposterior sensillary area, ending anteriorly in a variously shaped, usually denticulate tectum (epistome) bearing a single seta (2 in *Tr. camilla*; in *Ipotrombicula*, known only from the adult, there is an accessory seta at the base of the crista). Eyes if present single, either close to sensillary area, or lateral to crista and away from scutum; if absent may be represented by pigment spots.

Subfamily TROMBICULINAE Ewing

Diagnosis (slightly modified).—Trombiculids whose larvae have a single median scutal seta (‘AM’), no anterior projection (nasus) on the scutum, and no stigmata or tracheal trunks; femora of legs II and III only occasionally undivided (all legs usually 7-segmented.) Nymphs and Adults without dorsal stump-like process to tarsus; frequently with scutum relatively long compared with breadth.

Remarks.—The writer prefers to distinguish two broad generic groups in this subfamily, related respectively to *Trombicula* (with unexpanded sensillae) and to *Euschöngastia* (with terminally expanded sensillae), the latter group having a greater number of affinities with the Gahrlepiinae (=Walchiinae) in the presence of expanded sensillae, the presence of undivided femora in at least two different groups (*Walchiella* and *Pseudoschöngastia*), the relative frequency of multisetose coxae, and in the shape of the scuta of the nymphs and adults (resembling those of the Gahrlepiines in the genera *Guntherana* and *Dolosisia sens. lat.*).

A. *Trombicula* GROUP OF GENERA—FILIFORM SENSILLAE

Genus *Trombicula* Berlese 1905, expanded

Type.—*Trombicula minor* Berlese, 1905:155, *Redia*, 6, 346-388. Adults from bat-guano, cave in Java (types now destroyed).

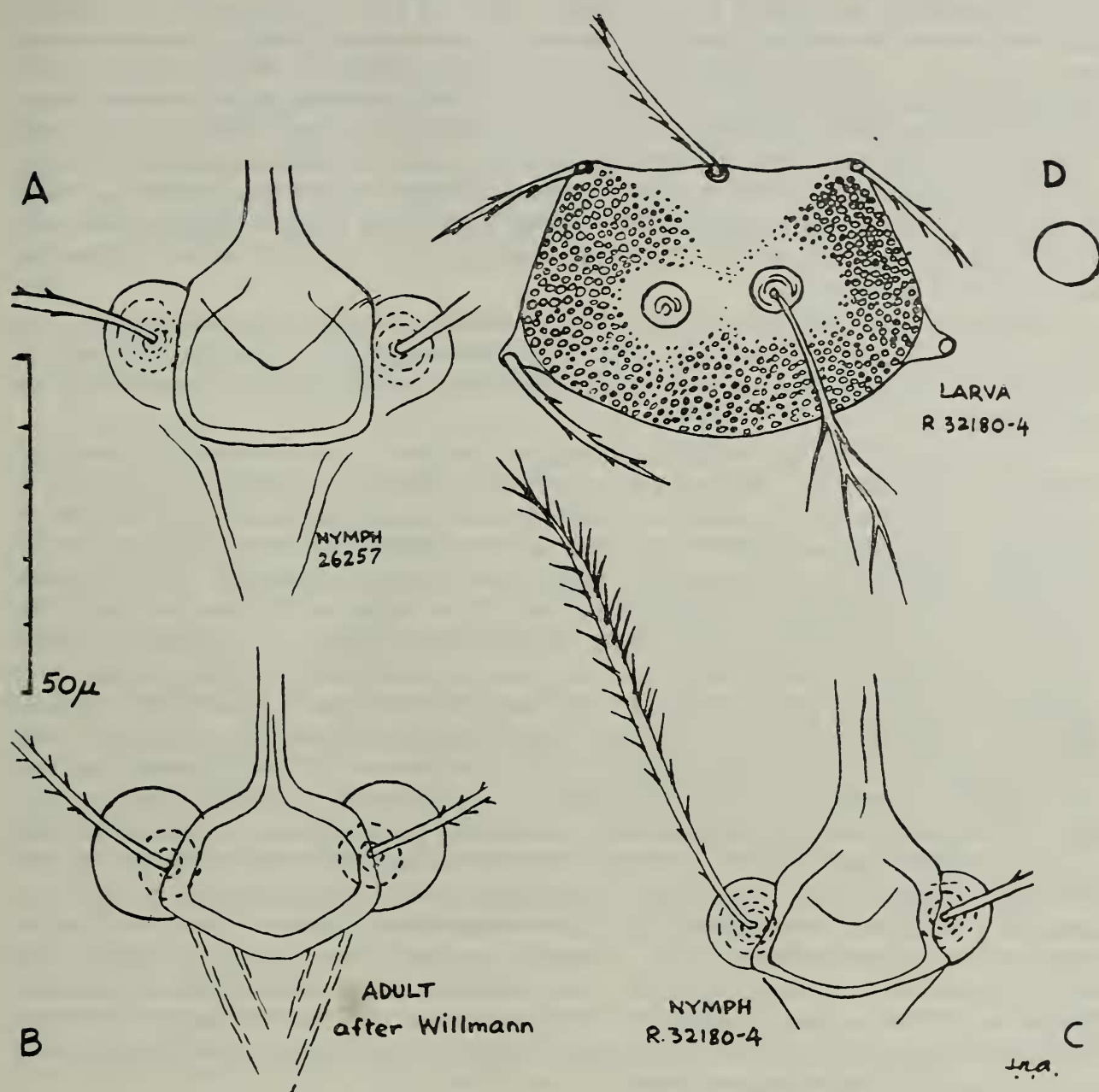
Provisional Diagnosis (tentative broad genus).—Trombiculines whose larvae have 5 scutal setae, unexpanded sensillae (mid-shaft occasionally slightly thickened, e.g. in *harrisoni*-group), only coxa III ever with more than one seta and that exceptionally, tarsal claws normal with slender clawlike empodium. Nymphs and Adults with generally elongate scutum, sensillary area roughly diamond-shaped, with roughly dumb-bell shaped areola; eyes when present either placed close to sensillary bases or lateral to crista and away from the scutum. Sternum entire, precoxal plates generally absent, but in subgenus *Leptotrombidium* precoxal plate of leg I present and fused to form a longitudinally subdivided sternum.

Remarks.—The type species is unknown in the larval stage, while its description in the adult stage is very incomplete. The type specimens, from a bat-cave in a remote part of Java, were destroyed by the bombing of Hamburg during the war. Dr. Cornelius B. Philip in March 1948 approached Dr. A. Diakonoff of the Zoologisch Museum en Laboratorium at Buitenzorg (now the Museum Zoologicum Bogoriensis, Bogor, Indonesia), but attempts to collect some more material in the type locality failed. Dr. Diakonoff has since been appointed to the Rijksmuseum at Leiden. The present writer recently attempted to get more material collected, but in a letter dated June, 1953, Dr. M. A. Lieftinck, Director of the Museum at Bogor, explains that "there are still difficulties in getting to the Tjiampia caves and I fear that there will be no chances of this at all since I have been informed that the bat caves at this locality are entirely spoiled, the fauna having disappeared almost completely. So there is no particular reason to visit the spot again, except for a pilgrimage. Since, as far as I know, there is no one in Indonesia working on Trombiculids at the moment, practically none of the former rich bat cave localities being at all accessible, I am afraid that I should not succeed in getting specimens for you from elsewhere."

Willman (1941) gave a redescription of the type together with drawings of part of the scutum and palps. Unfortunately there was at that time very little material available for comparison, so that the redescription is incomplete in the light of post-war studies. It is also important to note that the drawing of the parts of the scutum which Willman wished to discuss is semi-diagrammatic. Gunther (1951) has given a valuable review of the early descriptions of *minor*, and its later temporary confusion with the scrub-itch chigger *T. wichmanni*.

We know that *T. minor* is a very small species (adult about the size of most nymphs), and that being recovered from bat-guano the larvae are perhaps more likely to be found on bats than other animals; while we have an imperfect drawing of the scutum and palps, and meagre descriptions of features which are not of generic importance. The writer wishes to comment on two problems: the interpretation of the existing drawing and description of the type, and the best way of handling this difficult genus.

Womersley (1952:328) interprets the relatively large circles around the sensillary bases of *T. minor* (fig. 2) as being eyes which have been displaced so as to lie behind the sensillary bases. In this he differs from Ewing (1944) who believes that the circles represent chitinous rings. On this assumption Womersley erected his subgenus *Trombicula* which is in fact based on the post-larval characters of *T. wichmanni* and other species of *Eutrombicula*. The present writer doubts Womersley's interpretation of Berlese's and Willmann's drawings for the following reasons: (a) the bilateral symmetry argues somewhat against distortion and displacement; (b) taking the actual small size of the scutum into account, the "sensillary bases" as drawn are relatively much too small because these structures do not vary greatly in size as does the scutum generally; (c) the overlap between the edges of the sensillary bases and the intervening part of the scutum is taken by Womersley to be evidence of displacement of both sensillary bases and the "eyes" and so also is the eccentric origin of the sensillae themselves; but such a partial overlap may often be seen in specimens where the intervening sensillary area is convex, while even if there is displacement this still does not suggest the existence of eyes; and the eccentric origin of the sensillae is quite commonly seen; (d) the larvae of species which have been associated with *minor* in possessing eyes in the postlarval stages are bird and reptile chiggers (here treated as subgenus *Eutrombicula*) quite unlike any chiggers so far recovered from bats in this region; (e) three species of *Trombicula* now known from bats are very small, but not one resembles *Eutrombicula*; (f) two species of nymphs examined by the writer (fig. 2) show a sufficiently close resemblance to the drawing of *minor* to suggest that the larger circles drawn from type material are the rims of the sensillary bases and not



2. *Trombicula minor* and related species.

A, scutum of Nymph, *Trombicula* sp. (?*T. batui*) found in bat-guano, Malaya ; **B**, scutum of Adult of *T. minor*, after Willmann ; **C**, scutum of Nymph, and **D**, scutum of Larva, species near *T. minor* from bat, Malaya.

The original drawing (**B**) by Willmann is semi-diagrammatic and refers to an adult ; **A** & **C** are drawn somewhat similarly from nymphs for comparison. The inner line extending from the shaft of the crista and expanding into the areola in **B** shows structure lying deeply, the surface structure being omitted. This is in accord with the inclusion of the posterior apodeme which also lies deeply (see comments on structure of the scutum on p. 130). *Note* : In **D**, the PL setae can be seen placed on poorly chitinated extensions. In old mounts the edge of the almost-reticulated scutum is very distinct and only with difficulty, under phase-contrast, can this chigger be distinguished from species of *Tecomatiana*.

eyes. It would therefore appear that Ewing's interpretation of the circles in the original drawings is correct.

The following bat-chiggers are diminutive, similar in size to *Euschöngastia* (*Walchiella*) *oudemansi*, and of the order of size of *T. minor*: *T. minutissimum* (Ouds.) (distinctive larva, from Europe, see p. 147); *T. batui* Philip and Traub (also distinctive); *T. n. sp. R32181* Audy in MS (bred to the nymph, fig. 2). In addition to the last-named nymph, the writer recovered a single small nymph from bat-guano from a cave on Seletan Island. This cave had been occupied by tomb-bats, *Taphozous melanopogon*, from which *Trombicula taphozous*, *T. insolli*, and *T. batui* were recovered: the nymph is likely to belong to one of these species, and from its fairly small size it might even be *batui*. In fig. 2 the scuta of these nymphs have been drawn in outline for comparison with the reproduction of the scutum of *minor*, at about the same degree of enlargement.

The writer concludes that the genotype of *Trombicula* is without eyes in the nymphs and adults and that although assumptions as to close larval relationships cannot yet be made by comparisons of nymphs, the nearest relations so far found are the above new species (*R32181*) and probably *batui*.

Concerning the best way to stabilise this genus, Wharton and Fuller (1952:41) state that "Berlese's description and Willmann's redescription of the type indicate that *T. minor* is congeneric with the adults of larvae that will key to the genus *Trombicula* in the above key." This broad statement is acceptable but it must also be admitted that not enough is yet known of nymphs and adults to be confident of generic or subgeneric differences. The statement therefore does not exclude the possibility that any of the subgenera of *Trombicula* sensu lato may prove not to be congeneric with *minor*. These authors continue "In order to maintain stability in the use of *Trombicula* as a generic name, the subdivisions of this originally large genus are here considered as subgenera. The only other alternative would be to consider *Trombicula* as containing only the genotype until additional information is obtained. Such a course would be entirely unjustified since, despite the plethora of generic names that have been proposed, *Trombicula* as here understood is no broader in its content than are such genera as *Neoschöngastia* and *Euschöngastia*. In handling nomenclatorial problems of this kind stability should be maintained if it at all possible to do so and still remain in agreement with the known biological facts." The present writer agrees with the course suggested but would urge that a number of the subgenera should be recognised as genera whenever they can be clearly and unequivocally distinguished. *Fonsecia* is a case in point (see p. 148 below), while possibly *Eutrombicula* (see p. 145) may also justifiably be separated from *Trombicula*. *Blankaartia* (= *Tragardhula*) is probably a valid genus but until the confusion of larvae of *Blankaartia* with some of those of *Neotrombicula* can be satisfactorily cleared it is probably best to recognise *Blankaartia* as a subgenus.

Wharton and Fuller include in the subgenus *Trombicula* all the species which cannot definitely be grouped in the other subgenera, which they have in each case treated in a restricted sense (e.g., *Leptotrombidium* is practically restricted to the *akamushi*-group). The usefulness of this course is doubtful to the present writer, who would prefer to expand the concepts of the present subgenera and to avoid as much as possible deliberately making a nomenclatorial dustbin. Even if this is done, many species must at present remain unallocated and it seems best to recognise them as such rather than to force them into existing subgenera.

Subgenus **Leptotrombidium** Nagayo *et al.* 1916, sensu lato.

Type.—*Trombidium akamushi* Brumpt 1910:506, *Precis de Parasitologie*, 2nd. ed., Paris (915 pp.). Common and widespread on mammals and birds, especially in triangle Malaya-Japan-New Guinea.

Provisional Diagnosis (expanded).—Trombiculids whose larvae have roughly rectangular scuta, filiform sensillae with branches or barbs; palpal formula typically N/N/BNN(B) but setae on femur and/or

genu may be barbed; galeal seta nearly always branched or ciliated (but ?nude in *myzantha*); bases of chelicers typically angulated laterally (regularly in *akamushi*-group); no long outstanding nude or plumose setae on legs; larvae parasitic on mammals and secondarily to a limited extent on birds. Nymphs & Adults without eyes; precoxal plates to coxae I present (?always) and fused to form a longitudinally divided sternum. Womersley also describes a rectangular epistome with the anterior margin slightly concave or sinuous, finely denticulate; tarsi I are tapering, widest proximally.

Remarks.—This subgenus is usually taken to be synonymous with the *akamushi*-group. Womersley has restricted the larval diagnosis thus, but has accepted a number of species which fall outside it on larval characters but are included on nymphal characters. The present writer believes that there are good reasons for broadening this subgenus to include such species. The nearest relations appear to be the subgenera *Trombiculindus* and *Trombicula*, and certain unallocated species such as *T. jayewickremei* Wom., the nymph of which has no precoxal plates.

The angulation of the cheliceral bases was recorded as a character of the *akamushi*-group by Wharton (1946:173). It is occasionally present in unrelated chiggers, e.g. in some *Euschöngastia*, and may not always be present in species now included in the broad subgenus.

The diagnosis of the *akamushi*-group usually includes the specific palpal formula N/N/BNN. Species such as *T. palpalis* with palpal formula N/N/BNB are thus excluded. The writer has a specimen (species near *deliensis*) from Imphal with the palpal tarsus BNN on one side and BNB on the other. It is probable that too much insistence is placed on this feature, and that *palpalis* and related species should reasonably be placed in the *akamushi*-group. On the other hand, there is considerable variation in the scutal shape, one group showing a tendency for the PL setae to creep up the sides of the scutum away from its rounded posterolateral corners, so that the sensillary bases come to lie well behind the line of the PLs, as in *pallida*. This "*pallida*-subgroup" also shows a tendency to unusual development of the scutal (especially PL) and dorsal setae, with more or less thickening and development of heavy barbs (compare the blade-like processes of *T. baluensis* Traub & Audy, this *Study* p. 48). The members of the subgenus *Trombiculindus* (see below) have the same palpal formula (N/N/BNN) and scutal shape but the setal modification has gone much further: it is possible that there may be a close link here. With these considerations in view, we may attempt a tentative regrouping of the subgenus as shown in the following tabulation.

There is an indeterminate group comprising *jayewickremei*, *muscae*, *philipi*, *quadriense*, and *taphozous*, all of which appear to be related. All but *jayewickremei* are bat-chiggers. The nymph of *jayewickremei* has been described by Womersley under his subgenus *Neotrombicula*, without the fused precoxal plates. These species have the sensillary bases relatively close together considering the width of the scutum (cf. *gliricolens*, which Dr. Raja Varma has bred to the nymph and, in a personal communication, has placed in *Leptotrombidium*). They may be related either to *Leptotrombidium* or to *Trombicula*, probably the former.

**Old World species.*—Europe & U.S.S.R.: ?*muscae*, *russica*, *orientalis*, *pavlovskyi*, *subakamushi*. Africa: *le-gaci*, *natalensis*. Asia & Pacific: *akamushi* NA, *baluensis* T. & A., *bhimtalensis*, *bodensis* N, *burmensis* N, *burnsi*, *deliensis* NA, *dux*, *fuji*, *fulleri* N, *gliricolens*, *himizu*, *intermedia*, *keukenschrijveri* N, *kitasatoi*, *kuroshio*, *lanceolata*, *longiseta* N, *macacus*, *micula* T & A N, *miyairii*, *miyajimai*, *miyazakii*, *murotoensis*, *myzantha* N, *pallida* A, *palpalis*, *parapalpalis*, *pelta*, *pilata* T. & A., *pipellae* T. & A., *puta*, *robusta*, *scutellaris*, *sylvestris* N, *tarsala* T. & A., *tenjin*, *teramurai*, *tithwalensis*, *tosa*, *villosa*, *yasuokai*; *tanakariyoi*, *muridia*, ?*muscae*-group, *kawamurai*; 11 n. spp. to be described.

New World species.—*mexicana*, *myotis*, *panamensis*, *potosina*.

Subgenus *Trombiculindus* Radford 1948

Type.—*Trombiculindus squamosus* Radford 1948:126, *Proc. Zool. Soc., Lond.* 118, 213-272. From a rat, Himalayan range, India. —(continued on p. 143)

*In this and all following lists, the letters N, A following a name show that that species has been bred to the Nymph, Adult, to the writer's knowledge. Those with authors shown "T & A" are new species described by Traub & Audy, 1953, in this *Study*—See pp. 45-88.

TENTATIVE GROUPING OF *LEPTOTROMBIDIUM*

* Signifies that the nymph has been examined. Authors "T. & A." refer to species described by Traub & Audy, this *Study* p. .

1. **akamushi**-group sensu lato, palpi N/N/B(N?).N.N(B)

1.1 scutum normal, SBs in advance of or only level with PLs.

1.1.1 *akamushi*-subgroup

N/N/BNN

akamushi*bodensis***deliensis**pilalta* T. & A.**pipellae* T. & A.*scutellaris***sylvestris**villosa*

intermediate between 1.1.1 & 1.2.1:

*dux***fulleri***longiseta***micula* T. & A.*tarsala* T. & A.? *natalensis* (N/N/NNN)1.1.2 *macacus*-subgroup

N/N/BNB

*bhimtalensis**macacus*

?intermediate

puta (N/N/NNB)

1.2 PLs anteriorly displaced, SBs posterior to line of PLs

1.2.1 *pallida*-subgroup

N/N/BNN

(?related to *Trombiculindus*)*baluensis* T. & A.*burnsi**fuji**intermedia**kuroshio***keukenschrijveri**lanceolata**miyairii**miyazakii**murotoensis**pallida*? *tanaka-ryoi**teramurai**tosa*1.2.2 *palpalis*-subgroup

N/N/BNB

*himizu**palpalis**parapalpalis**tithwalensis**yasuokai*? *potosina* (N/B/NNB)? *miyijimai* (N/N/BBB)2. **burmensis**-group and ?others palpi B/B-N2.1 *burmensis*-subgroup

B/B/BNN

burmensis*muridia*? *miyajimai* (N/N/BBB)2.2 ?*robusta*-subgroup

B/B/NNN

myzantharobusta***gliricolens* (B/B/NNB)*pelta* (B/B/NNB)? *muscae*, ? *philipi*,? *quadriense*, ? *taphozous*

3. ??Other species, nymphs of which do not have the fused precoxal plates (some of the species listed above and known only as larvae may belong to this indeterminate group)

? *jayewickremei* (B/B/NNB)

Provisional Diagnosis (expanded).—Trombiculids whose larvae are similar to those of the *Trombicula* (*Leptotrombidium*) *pallida* subgroup (see above), but have at least the PL scutal setae and the anterior dorsal setae modified by replication or expansion (foliate). Nymphs & Adults (known only for 2 species here included for the first time in this subgenus) differing from those of *Leptotrombidium* in having no precoxal plates and in having the tectum (seen in one species only) convex instead of flat or concave distally.

Remarks.—Foliate setae have been developed in a number of unrelated groups so that a *Trombicula* might be found with foliate setae but *not* closely related to the type *T. squamosus*. To the writer, the important character is not leaf-like expansion of the setae, but simply their *modification*. The exact form of modification may vary considerably (contrast the setae of *cuneatus* with those of *squamosus* and *foliatus*). He would therefore include such species as *T. hastata* (Gater) (slightly foliate setae), as well as *T. fordii* Wom., *T. traubi* Wom., and *T. plumosa* Rad., in which the setae are otherwise modified. Shorn of their ornamental setae, all larvae appear to be indistinguishable from those of the *pallida*-subgroup. The nymphs of *hastata* and *fordii* have been described. It will be interesting to see what the nymphs of the fully foliated species are like.

World species (Asia & Pacific).—*cuneatus*, *foliaceus*, *fordii* N, *hastata* N, *plumosa*, *squamifera*, *squamosus*, n. sp. from Thailand (being described). Also *kansai* Jam. & Sasa, 1953.

Subgenus *Neotrombicula*, Hirst 1915

Type.—*Acarus autumnalis* Shaw, 1970, in Shaw & Nodder, *Vivarium Naturae, or, The Naturalist's Miscellany*, London; vol. 2, next to plate 42.

Provisional Diagnosis (sensu stricto, quoted from Wharton & Fuller 1952:56). —“ *Trombicula* in which the larvae have a pentagonal scutum, at least one mastitarsala III, normal scutal setae, and either nude whip-like or elongated feathered setae on some of the segments of leg III other than the tarsus. Adults elongated and without eyes.”

Remarks.—The type species *T. (N.) autumnalis* belongs to a distinct group with roughly pentagonal scuta and long setae which are nude, ciliated, or lightly plumose on the legs, especially on the more proximal segments. All the North American species have more than one mastitarsala III. It is difficult at present to separate this larval group from the larvae of *Blankaartia* (= *Tragardhula*). Brennan & Wharton (1950:44) in dealing with larvae of *Neotrombicula* in North America separate the two as follows:

Larvae with subequal plumose setae on the proximal segments leg III; usually parasitic on water birds; adults with eyes.

Tragardhula = *Blankaartia*

Larvae with whiplike or long plumose setae on the proximal segments of leg III; usually parasitic on terrestrial animals, especially small mammals; adults without eyes.

Neotrombicula

Womersley has however described this subgenus on the characters of nymphs and adults, which produces a much larger assemblage, the larvae of which are very heterogeneous. There are some very perplexing anomalies in this broad subgenus, suggesting that our ideas of what is or is not taxonomically important in post-larval characters may need drastic revision. The following species are included in this subgenus by Womersley:

- (a) Species known from Larvae & Nymph/Adult: *autumnalis*, *consueta*, *fordii*, *goldii*, *harrisoni*, *hastata*, *inopinatum*, *jayewickremei*, *parmifera*, *rara*, *sarcina*, *scincoides*, *spicea*, (also n. sp. near *rara*, in MS).
- (b) Species known only from Nymph/Adult, larvae unknown; *camilla*, *canestrinii*, *cavernarum*, *clavicata*, *coarcata*, *formicarum*, *manriquei*, *moesica*, *?russica*, (Vitzthum 1932, not Oudemans 1902; larva apparently unknown).
- (c) Species of larvae tentatively included by close resemblance to members in group (a): *kohlsi* (cf. *scincoides*), *munda* (cf. *spicea*), *tovelli* (cf. *scincoides*), *traubi* (cf. *fordii*).

Some of the many anomalies resulting from this grouping under the broad "post-larval" subgenus are noted below:

- (i) Species *fordi*, *hastata*, and *traubi*, with foliate or otherwise peculiarly modified dorsal setae, are not properly separable from *Trombiculindus* which is recognised as a subgenus by Womersley (see p. 141 above).
- (ii) The writer would ascribe the larvae of *goldii* and *scincoides*, as well probably as those of *kohlsi* and *tovelli*, to subgenus *Eutrombicula* (=subgenus *Trombicula*, Wom. partim). Similarly larvae of *sarcina* would be thus accommodated, because of their close relationship with larvae of *samboni*; but the nymphs and adults of *samboni* appear to be typical *Eutrombicula* (*Trombicula* of Womersley) and those of *sarcina* typical *Neotrombicula*. Wharton & Fuller (1952:47, 48) list *goldii* and *sarcina* under subgenus *Eutrombicula*; but they also include *coarctata*, known only from the adult.
- (iii) The larva of *jayewickremei* appears to be inseparable from those of some members of the subgenus *Leptotrombidium* sensu lato.
- (iv) As described elsewhere (Traub & Audy, 1953, this *Study* p. 48), there is a distinct group now recognisable related to *T. densipiliata* Walch. The nymphs of one member of this group are very close to that distinctive species *canestrinii*, known only from the adult. But the larvae are obviously different from those of the type, *autumnalis*. The same applies to such species as *spicea* and members of the *harrisoni*-group, which have larvae quite unlike those of *autumnalis* but have nymphs included in Womersley's broad subgenus.
- (v) Womersley has also described the nymph of *Heaslipia gateri* and states that this cannot be distinguished clearly from nymphs of his subgenus *Neotrombicula*.
- (vi) Species such as *T. flagellifera* Traub & Audy 1953 and *T. tuhana* Traub & Audy 1953 (pp. 46, 53, 55), have leg setae suggestive of *Neotrombicula* but their scuta and to some extent their palpal setation resemble those of *Leptotrombidium* spp.

It may be that many or even most of the species included in the broad subgenus by Womersley on account of post-larval characters should in fact be included in the subgenus *Trombicula* as provisionally redefined in the present paper. This course was not open to Womersley because he interpreted the existing drawings of *T. minor* as definitely showing the presence of eyes. As we have suggested, this interpretation may readily be a mistaken one. The present writer is not prepared to resolve any of these difficulties. It does however appear that the broad subgenus based on post-larval characters is not wholly natural. There may of course be convergence of polyphyletic groups of larvae in one direction, and of their corresponding postlarval stages in another, but this has not yet been demonstrated.

It would appear to be a sound step at this stage to recognise a true subgenus *Neotrombicula* sensu stricto, including only those species which are clearly related to the type in both larvae and nymphs, and to divide Womersley's remaining species into two groups, (a) those which appear to have sufficiently close affinities with *minor* to be included provisionally in the subgenus *Trombicula* pending further studies, and (b) those which cannot confidently be relegated to either group but which have affinities with both on the characters of nymphs and adults. This last group may be provisionally considered as ?*Neotrombicula* or ?*Trombicula* and in the lists of Old World species given by the present writer he has attempted to relegate certain species to one or other subgenus on fairly arbitrary larval characters. He does this without much confidence, but in the belief that this is one more step in the right direction.

At the same time, as many small species-groups as possible should be recognised. This has been done for the subgenus sensu stricto by Brennan & Wharton (*loc. cit.*) who have

picked out three groups, the *autumnalis*-, *microti*-, and *bisignata*-groups, characterised by the nude flagellate setae of leg III as follows (some species are ungrouped):

<i>Neotrombicula</i> .	Mastitarsala. Mastitibiala. Mastifemorala.				
<i>autumnalis</i> -group (Old World)	I	...	O	...	O
<i>microti</i> -group (New World) ...	2	...	I	...	I
<i>bisignata</i> -group ...	3	...	I	...	O

Old World species of Neotrombicula sensu-stricto.—Europe: *autumnalis*, *desaleri*, *fahrenheitzi*, *muris* (Ouds.), *pomeranzevi*, Asiatic-Pacific: *fugjimo*, *japonica*, *mitamurai*, *nagayoi*, *tamiyai*, *AX*-group (*kashmirensis*, *kanzalwanensis*, *AX* n. sp. Wom., & Audy in MS).

Old World species which may or may not be related: possibly some of those known only as adults or nymphs; possibly the *flagellifera*-*tuhana* group [see (vi) above]; possibly *naultini*, *novae-hollandiae*.

Subgenus **Blankaartia** Oudemans, 1911

=**Tragardhula** Berlese, 1912, Wom. 1948

=**Pentagonella** Thor, 1936

=**Megatrombicula** Michener, 1946

Type.—*Trombidium niloticum* Tragardh 1904:78, *Results Swedish Zool. Exped. to Egypt and the White Nile*, 1901, 20, 1-124. Adult only, from water-plants, Egypt.

Diagnosis.—Species of *Trombicula* whose larvae have a pentagonal scutum, at least one mastitarsala III but, unlike the similar larvae of *Neotrombicula*, do not possess mastifemorale and/or mastitibiale III or long lightly-feathered setae in the place of these; apparently swamp or water-frequenting, particularly parasitising water-birds*. Nymphs & Adults distinguished by having a pair of eyes lateral to and some distance from the crista (not near the sensillary bases as in *Eutrombicula*).

Remarks.—It is necessary to regard *Blankaartia* as a subgenus until its relationships with *Neotrombicula* are satisfactorily clear. *Blankaartia* may for example have developed by its special habitat adaptations from a *Neotrombicula* stem. The correct usage of *Blankaartia* instead of *Tragardhula* (used by Womersley) has been discussed by Fuller & Wharton (1952). Of the 14 species listed by Womersley (who omits only the African *T. ardeae*) five are known as larvae & nymphs/adults, viz. *acuscutellaris*, *alleeii*, *attenuata*, *japonica*, *velascoi*, and two (*nilotica*, *peruviana*) as adults only. The present writer agrees with Wharton and others in placing *fugjimo*, *japonica*, *mitamurai*, *nagayoi*, and *tamiyai* in *Neotrombicula*. The remainder (*geckobia*, *gymnodactyla*, *pentagona*), all from reptiles, have 2-pronged palpal claws (undoubted *Blankaartia* species have 3) and no mastitarsala III—these form a distinct group (possibly including *incurva* & *naultini*) the relationship of which to the African *lawrencei* group (p. 147) should be investigated.

Old World species.—U.S.S.R.: *radfordi*, Africa (Egypt): *ardeae*, *nilotica* A. Asia & Pacific: *acuscutellaris* NA.

Subgenus **Eutrombicula** Ewing 1938

Type.—(*Trombicula flui* van Thiel 1930, Ewing 1938:293. *J. Wash. Acad. Sci.*, 28, 288-295; synonym) = *Acarus batatas* Linn. 1758:617. A common scrub itch mite: major hosts birds, Brazil to southern U.S.A.

Diagnosis (largely after Fuller 1952:96; = most of subgenus *Trombicula* Wom. 1952:326).—Trombiculids whose larvae have moderately large scuta, roughly rectangular, posterior border often slightly convex, usually distinctly punctate; leg III with a mastitarsala, possibly mastitibiala also; palpal claw 2-pronged, with the accessory prong medial or ventromedial to the axial; galeal seta generally nude; generally parasitic on reptiles and birds but may be on mammals. Nymphs & Adults of *Trombicula* facies but typically with eyes present, close to and slightly behind the sensillary bases (insistence on this character might be a mistake, as discussed below).

Remarks.—This has all the appearances of being a good larval genus on morphological as well as bionomic grounds, but its limits cannot yet be clearly defined. The writer suspects that the mastitarsala III and the general host-preference for reptiles and birds may be more important than details of the palpal claws. Putting aside Womersley's interpretation of *minor*

* In our collections, *acuscutellaris* appears to be associated with ricefields which are annually flooded. It is found on the ricefield-rat *R. rattus argentiventer* in suitable localities.

(see p. 138 above), he lists (his p. 327) the following nymphs/adults under the same group characters: (a) *frittsi*; (b) *alfreddugesi*, *batatas*, *helleri*, *samboni*, *splendens*, *vanommereni* Schierbeek, *wichmanni*; and (c) *jacoti* (nom. nov. for *Trombiculoides scaber* Jacot 1938). The last may be ignored because the larva is not known: Jenkins (1949:294) was unable to find differences between adults of *splendens* and adults identified as *jacoti* (*scaber* syn.). The larvae of *T. frittsi* are found on reptiles and a rat in the Pacific area, and (assuming a correct identity with the Malayan species from which the nymphs were bred) scorpions in Malaya; the mastitarsala III is absent and the scutum is small and pentagonal. There are many features distinguishing it from larvae of *Eutrombicula*. Furthermore the scutum of the nymph is relatively shorter than in those of group (b) while the sensillae have thickened shafts. The presence of eyes in the nymphs does not warrant including *frittsi* in this species-group: as discussed below, it may be close to *Fonsecia*.

Of the remainder, (b), the larvae are all typical *Eutrombicula*, but (i) the larva of *vanommereni* cannot be separated from that of *alfreddugesi*, of which it is now regarded as a synonym, and (ii) the larva of *helleri* can hardly be separated from that of *goldii*, of which it is regarded as a synonym*—but the adult of *goldii* is described by Womersley (p. 370) under the subgenus *Neotrombicula* as without eyes (quoting description of Boschell & Kerr 1952). This is particularly interesting because the nymph of *sarcina* is also without eyes (described under *Neotrombicula*, Wom. 1952:362), although the larva appears to be typical *Eutrombicula*. It is an amusing question as to whether we are dealing with evolutionary convergence among larvae or divergence among adults; or possibly with rudimentary eyes which require fresh material and a phase-contrast microscope for their detection. The present writer is unable to offer a worthwhile opinion. It is however likely that attempts to take post-larval characters too seriously at this early stage will often lead one astray. The writer therefore proposes to accept a group of *Eutrombicula* which do not appear to have eyes in the adult state. (It is worth noting that of three nymphs of *Eusch. lacunosa* bred out from the same *Rattus bowersi* in Malaya, one was pinkish and showed conspicuous scarlet eyespots while the other two were white and without eyespots; no eyes were however visible in any specimen after mounting. The larval pelts were indistinguishable on first examination).

African species described in this genus by Lawrence (1949:441-449), and listed under the subgenus *Eutrombicula* by Wharton & Fuller, cannot be included (Lawrence characterised the genus by the number of dorsal setae, after Ewing). Lawrence's species fall into two groups, both with 3-pronged palpal claws: (a) an *ilesi*-group from African reptiles, with pentagonal scuta, probably related to *frittsi*, comprising *aenigma*, *homopholis*, *montensis*, *rhodesiensis*, *rhopropi*, to which we should add *T. nivaria* Law. and *T. ilesi* Rad; and (b) a *lawrencei*-group, also from reptiles, with convex but not angulated posterior scutal margin, comprising *lawrencei* Wh. & F. (= *agamae* Law. preocc.), *draconensis*, *gerrhosauri*, *pachydactyli* (and ?*abyssinica* from a bird). The two groups appear to be related to each other but not to *Eutrombicula* as here defined: it may however be that this subgenus has been considered too rigidly. As discussed below, the *ilesi*-group seems to be closely related to the genus *Fonsecia* and the matter demands study. The African *lawrencei*-group may be related to the Australasian *geckobia*-group (p. 148). Without material for comparison, the writer is unable to place *E. jadini* Verc. 1953.

Jenkins (1949) & Wolfenbarger (1952) have made important studies of this subgenus in America.

Old World species (Asia & Pacific).—? *cervulicola*, *hirsti* (?= *wichmanni*) N, *isshikii*, *lygosomoides*, ? *macropus*, ? *nautilini*, ? *novae-hollandiae*, *rioi*, *samboni*, *sobrina*, *wichmanni* NA, *sarcina* (with eyeless nymphs) N; possibly related (no mastitarsala III in larvae, no eyes in nymph): *scincoides* N, *kohlsi*, *tovelli*. Also, *lumsdeni* & *watsoni* Rad. 1953.

* The probable identity of *helleri* with *goldii* is carefully discussed by Fuller (1952:141), who also (p. 117) discusses differences between *vanommereni* and *alfreddugesi*.

Subgenus **Trombicula** Berlese 1905including subgenus *Neotrombicula*, Wom. 1952, *partim*.

Type.—*Trombicula minor* Berl. 1905:155, *Redia*, 6, 346-388. Genotype; adults only from bat-guano, Java.

Provisional Diagnosis (restricted).—Larvæ without the combinations of characters of the other subgenera; scutum not broadly rectangular, but more nearly quadrate or trapezoidal, posterior margin convex (scutum almost bluntly pentagonal) or emarginate and medially convex (sinuous); sensillary bases fairly close together (SB less than $2/3$ AP); no long nude setae on legs; parasitic on mammals (type is a very small species presumably parasitic on bats.) Nymphs & Adults of typical *Trombicula* facies, without eyes (type adult very small).

Remarks.—The probable relationships of *T. minor* have already been discussed. The writer is well aware that the diagnosis given above is based on tenuous concepts. Its object is to prevent the subgenus from being used too freely as a depository for unallocated species, the writer preferring to leave such species unallocated *sub judice*. Until something better is found the writer proposes to take the new Malayan bat-chigger which has been bred to the nymph (fig. 2) as a model around which to frame this subgenus. There are good reasons to suppose that it is congeneric with *minor*. By adopting a model which can be described in detail in both larva and nymph, it will at least be possible to build up a consistent subgenus, even if it may later prove to be the wrong one (which however is most unlikely).

Those species known only from the adult and listed by Womersley under *Neotrombicula* should be held unallocated until they can be surely placed in *Trombicula*, *Neotrombicula*, or another subgenus; the cavernicolous species in particular may belong to *Trombicula*. These species are: *camilla*, *cavernarum*, *clavicata*, *coarctata*, *formicarum*, *manriquei*, *moesica*, ?*russica* Vitzthum, 1932 (not Ouds. 1902; this adult cannot be identified with either *russica* or *muscae* and its name may be homonym, but it might as well be left as it is for the time being).

Microthrombidium minutissimum Ouds. 1910:104 (*Ent. Ber.*, *Amst.*, 3, 103-109) from a bat in South Africa, has been redescribed by Fuller (1952:86) and we may note those characters which may be of subgeneric importance: small chiggers with a small scutum (AW 30-45 μ or less) which is nearly as deep as broad. AM advanced in front of line of ALs (anterior margin is triangular in *minutissimum*). Sensillae simply forked (or ? with very few subequal barbules). The advancement of the AM seta may readily be exaggerated in this particular chigger (cf. species of *Dolosisia* sens. lat., p. 157) and it probably cannot be regarded as a subgeneric character even though in this species it gives a very distinctive inverted-pentagonal shape to the scutum. Allowing for this, the peculiar forked sensillae and the general shape of the scutum suggest a relationship with the bat-chigger *T. batui*. There also appear to be close relationships with *T. munda* and with several African chiggers related to *T. panieri* Jad. & Verc. 1952, viz., *giroudi*, *panieri*, & *rodhaini*, as well possibly with *T. schmitzi* (which has barbed sensillae).

Speleocola Lipovsky 1952 was raised to accomodate a peculiar chigger (*S. tadaridae*) from the ears of molossid bats in Oklahoma. The edges of the scutum are obscured by the attachment of cuticular striae, and the somewhat fusiform sensillary shafts are clothed in expanded setules which gives the sensillae an appearance of being lanceolate. The relations of this very interesting genus to *T. spicea* should be investigated.

Because the writer has yet had no opportunity to make a careful study of them, the species listed below are offered only as suggestions for investigation. The list includes a number of bat-chiggers, which is an interesting coincidence because the species have not been chosen for their host preferences.

Old World Species (tentative).—Europe: *minutissima*. Africa: ?*T. panieri* group (*cynictia*, *giroudi*, *panieri*, *rodhaini*). Also ?*mastomyia*, No. CORU36696 n. sp. (in *harrisoni*-group; bat, S.W. Africa). Asia & Pacific: *batui*, ?*insolli*, *minor* A, *munda*, *piercei*, ?*schmitzi*; *T. harrisoni* group (all from bats—*dimolinae*, *harrisoni* N, R17289 n. sp. Malaya). ?*T. spicea* group—? *buxtoni*, ?*khurdangensis*, *rajoriensis*, *spicea*.

Unallocated species of *Trombicula*

An attempt has been made to collect the remaining species into as many species-groups as possible. There is no doubt that many more groups will be discovered by further study. The groups presented are mostly tentative and have not been investigated deeply. Attention is drawn to the *Trombicula cynos* group described by Brennan (1952): many more studies like this are badly needed in this region.

anous-group: *anous*, *pluvius*.

geckobia-group (Asia & Pacific; almost pentagonal scutum, on reptiles; see p. 146): *incurva*, *geckobia*, *gymmodactyla*, *?naultini*, *pentagona*.

ilesi-group (Africa; pentagonal scutum; on reptiles; may be related to *Fonsecia*; see below): *aenigma*, *homopholis*, *ilesi*, *montensis*, *nivaria*, *rhodesiensis*, *rhoptropi*; *?frittsi* (Malaya, Australia).

lawrencei-group (Africa; ?related to *geckobia*-group, see p. 146): *lawrencei*, *draconensis*, *gerrhosauri*, *pachydactyli*.

leveri-group (bats): *leveri*, *revelae*.

muscae-group (bats; p. 141): *muscae*, *philipi*, *quadriense*, *taphozous*.

parmifera-group (almost pentagonal scutum, on reptiles): *parmifera*, *lundbladi*, "MAB" n. sp. in MS.

rara-group (AW:SB about 5-6:4; on reptiles, arthropods): *rara*, n. sp. nr. *rara* from pill-millipede (Wom. & Audy in MS); *?thori*.

vorca-group (mostly on birds): *?corvi*, *?canestrinii*, *densipiliata*, *nissami*, *?strinatii*, *vorca* Traub & Audy 1953 (this *Study* p. 48) (& *thompsoni* Brennan from U.S.A.).

Ungrouped species.—Europe: *clavicata* A, *formicarum* A, *moesica* A, *vernalis*, *willmanni* W. & F. (= *multisetosa* Will.), *zachvatkini*. Africa: *boaedonia*, *bruynoghei*, *centropodis*, *claviglia*, *claviglicola*, *guineense*, *jadini*, *microps*, *nigeriensis*, *praomyia* (p. 160), *rhodesiana*, *scapulosa*, *sicei*, *subquadrata*, *sulae*, *tragardhi*. Asia & Pacific: *ablephara*, *consueta* N, *jayewickremei* N (p. 141), *jubbulporensis* (see p. 160), *kalrae*, *southcotti*, *vietzi*; *agamae* André.

Genus *Fonsecia* Radford 1946

Type.—*Trombicula ewingi* Fonseca 1932:153, *Mem. Inst. Butatan S. Paulo*, 7, 151-158. From a snake, Brazil.

Diagnosis.—*Trombiculines* of the *Trombicula* group whose larvae have at least the anterolateral scutal setae (ALs) modified by reduction to peglike or short expanded processes; scutum shield-shaped, roughly as broad as deep, bluntly pentagonal; parasitic on reptiles, possibly exclusively on snakes.

Remarks.—A new species from Malaya is being described (Audy 1955, in MS) in which the modification of the setae is carried on to involve the PL setae and the anterior rows of dorsal setae as well. The AL setae are peculiarly modified in a way suggestive of those of *F. travassosi* Fonseca. The PL setae and anterior dorsal setae are modified more simply by basal swelling, like the setae of *Euschöngastia causicola* (Jadin & Verc.). This group is sufficiently distinct in both morphology and host-preference to be recognised as a genus. It appears to be closely related to the *ilesi* group (*T. ilesi* itself also being from a snake) and indeed the two groups may later prove to be congeneric.

The modification of these setae is extremely interesting. There are very many examples to show that the PL scutal setae and the anterior dorsal setae are genetically linked and develop under the influence of the same organiser (using this term in the embryological sense). When setal modifications in this PL-DS field are extensive, they may involve the AL setae also, but rarely the AM. The genus *Fonsecia* illustrates modification of the other organiser field, the ALs alone being modified in *ewingi* & *coluberina*, and both ALs & AM in *travassosi*, while the extensive modification in the new Malayan species secondarily involves the PL-DS field in producing a less developed modification of those setae, while the AM seta is unmodified. A study of the many chiggers with foliate setae shows that modification in the PL-DS field does not usually extend to those post-and para-anal setae which we describe as "caudal setae" (CS), where presumably the influence of the VS-field is felt. Similarly, the humeral setae (HS) which often differ from the dorsal setae in both larvæ and nymphs, appear to be influenced by the coxal field (we may note the tendency for multisetose coxae to be associated with multiple humeral setae, e.g. in *Dolosisia* sensu lato, p. 157).

The inference is that, being influenced by different organiser fields, the detailed differences between the AM-AL, the PL-DS, the humeral setae (HS), the caudal or postanal setae (CS), and the ventral setae (VS) are of taxonomic importance, and there is support from several sources for the plea made by Audy (1952) that the caudal setae be compared with and enumerated separately from the ventral setae. A further inference is that the PL setae virtually represent dorsal setae but are customarily placed on the scutum. The retraction of the scutum to isolate these setae, or its extension so as to include extra dorsal setae, may be reasonably anticipated; and of course it does occur.

World species.—Asia: *coluberina*, CORU.35961 n. sp. Audy in MS. South America: *ewingi*, *travassosi*.

Genus **Tecomatlana** Hoffman 1947

including **Sauriscus** Lawrence 1949

Trisetica Traub & Evans 1950

Type.—*Tecomatlana sandovali* Hoffman 1947:452, *An. Escuela nac Cienc. biol., Mex.*, 4, 451-457.

Diagnosis.—Species related to *Trombicula*, whose larvae have the PL setae displaced off the scutum.

Remarks.—*Sauriscus ewingi* Law. is from lizards in Africa; it has a shallow scutum, finely barbed sensillae, single eyes, a 2-pronged palpal claw. *Trisetica melvini* Traub & Evans is from a bat-cave in North Burma; it has a deeper scutum, a peculiar thickened sensilla, double eyes, slender elongated claws with 3 subequal prongs. *Tecomatlana sandovali* is from bats in Mexico; it has a scutum like that of *melvini*, but normal sensillae with barbs in the distal half, a short axial prong and 3 short accessory prongs to the claws. The writer believes that it would be a mistake to assume that these three must be congeneric simply because they share a recurrent character (PLs off the scutum) which might have developed independently from unrelated progenitors. He therefore intends to preserve *Sauriscus* and *Trisetica* as subgenera until further studies clarify matters.

Genus **Myotrombicula** Womersley & Heaslip 1943

Type.—*Myotrombicula vespertilionis* Wom. & Heaslip 1943, *Trans. R. Soc. S. Aust.*, 67, 68-142. From bats, Australia.

Diagnosis.—Monotypic: Larva with broad shallow scutum but nature of sensillae not known; cheliceral blade modified (short, stumpy, with two large blunt teeth); palpi somewhat modified (laterally angulate, strongly incurved).

Remarks.—Wharton & Fuller (1952:84) state that "if the type species has expanded sensillae, *Myotrombicula* might be a synonym of *Oenoschöngastia*," but the present writer would not subscribe to this view because *Myotrombicula* has a completely different shape of scutum, no mastitarsala III, and the chelicers are differently modified: there are probably a number of other differences, e.g., in the leg chaetotaxy.

Genus **Heaslipia** Womersley 1952

Type.—*Trombiculoides gateri* Wom. & Heaslip 1943:101, *Trans. R. Soc. S. Aust.*, 67, 68-142. From rats, highlands of Malaya.

Diagnosis.—Monotypic: larva with scutum not extended posteriorly but including additional setae (4); mastitarsala III present. Nymph of typical *Trombicula* (*Neotrombicula* of Womersley) facies, without eyes, and a large triangular tectum.

Genus **Novotrombicula** Womersley & Kohls 1947

Type.—*Novotrombicula owiensis* Wom. & Kohls 1946:4, *Trans. R. Soc. S. Aust.*, 71, 2-12. From soil, island off New Guinea.

Diagnosis.—Monotypic: larva with scutum extended posteriorly, with unexpanded sensillary bases anteriorly placed, and (2) additional posterior scutal setae (i.e., more than the usual 5) as in *Schöngastiella* and *Gahrlepiea*; mastitarsala III absent.

Remarks.—*Novotrombicula* and *Heaslipia* have a major character (additional posterior scutal setae) in common but this has clearly developed independently. The anterior part of the scutum of *Novotrombicula* resembles that of *T. rara* and *T. thori*, common on skinks, in the placing of the sensillary bases; this and the absence of a mastitarsala are probably of generic importance.

Genus *Ipotrombicula* Womersley 1952

Type.—*Trombicula elegans* Wom. 1942:173, *Rec. S. Aust. Mus.*, 7, 169-181. Adults only; sea-shore, Australia.

Diagnosis.—Monotypic, adults only: as described by Womersley 1952:323, *Rec. S. Aust. Mus.*, 10, 1-435.

B.—*Schöngastia* GROUP OF GENERA—EXPANDED SENSILLAE

Genus *Schöngastia* Oudemans, 1910

Type.—*Thrombidium vandersandei* Ouds., 1905:216, *Ent. Ber., Amst.*, 1, 216-218. From man, rats, birds in eastern Indonesia, New Guinea, Solomon Is.

Diagnosis (restricted).—Trombiculines whose larvae have 7-segmented legs; shield-like scutum with markedly convex posterior margin, 5 scutal setae, sensillary bases fairly close together, and globose sensillae; a series of teeth on the chelicers (which are usually long), and a nude seta or mastitarsala on tarsus of leg III (?? may not always be present); apparently restricted to the Old World tropics and sub-tropics; primarily parasitic on reptiles and often on birds, sometimes extending to mammals and including two important scrub-itch mites. Nymphs and Adults (known from 2 or 3 species: *schuffneri*, *vieta*, *maldiviensis*) without eyes, with the sensillary area about as wide as long, roughly triangular with apex directed backwards, SB relatively fairly wide (ASL/SB ratio 2); tectum rounded; sensillae nude or lightly barbed; precoxal plates present on coxae I. Not recorded from the New World.

Remarks.—This genus has been "defined" on a key-character (toothed chelicers) instead of being based on relationships with the genotype. What appears to be a good natural group of (larval) generic status has thus been confused by the inclusion of outsiders. It seems best to restrict the genus as rediagnosed above to the clear group-characters of the *vandersandei* species-group, viz., the triad, scutal shape, toothed chelicers, and mastitarsala III, added to the general host-preference for birds and reptiles. The general appearance of the scutum closely resembles that of the *lanius*-group (new subgenus *Helenicula* below). Dr Lawrence (in correspondence) describes a mastitarsala III near the base of the joint, clearly visible in his *S. platysauri*, *S. pseudocordyli* and *S. scincicola*, but he could not see this in the other species (see lists below). Varma (*in litt.*) is describing a new *Schöngastia* from near Calcutta: it has the typical almost-pentagonal scutum and the mastitarsala.

There is no doubt that a large number of ill-sorted chiggers are related to *Schöngastia* and Womersley has made this a major genus sensu lato. The writer feels that this group is well characterised in the larvae and is not the best choice as the typical subgenus of a heterogeneous group which is almost certainly destined to be split up into several genera in spite of apparent similarities between the post-larval stages. He therefore prefers to recognise *Schöngastia* sensu stricto and *Euschöngastia* sensu lato, the latter including a heterogeneous collection and corresponding to the other heterogeneous genera *Trombicula* sensu lato, *Gahrlepiea* sensu lato.

Three species at least (excluding Lawrence's species ? without mastitarsalæ, noted above, which require close study) are not congeneric. *Schöngastia oudemansi* Gater is quite distinct on a number of characters and while approving of Fuller's action in placing it in a new (and at the time monotypic) genus, *Walchiella*, it is unfortunate that this particular name was chosen because for reasons already discussed we cannot attach sufficient importance to the number of leg-segments to include this species in the *Gahrlepieinae*: its affinities are clearly with *Euschöngastia* (see p. 153 below).

Womersley's species *bidentata*, of which Mr Womersley has kindly sent us a specimen, is very distinctive and not congeneric: it must be accommodated in *Euschöngastia* despite the blunt

teeth on the chelicer, the presence of which alone is not a generic character. Similarly, *S.(S.) oculicola* Wom. 1952 is not congeneric and as discussed elsewhere (below, and by Audy, in MS) it is probably best accommodated in *Doloisia* sensu lato because in larva and nymph it shows much closer affinities with this genus than it does with the type of *Euschöngastia*.

Of species in Wharton and Fuller's list, *S. jamesi* Gun. is a synonym of a true *Neoschöngastia*, *N. yeomansi* Gun.; and *S. katonis* Wom and Heaslip is a synonym of *S. schüffneri* (vide Womersley, 1952:257, 159). These authors synonymise *blestowei* Gun. with *vandersandei*, and *S. maldiviensis* Rad. with *S. vieta* but Womersley retains these as species. In the case of *maldiviensis* there appear to be differences in both larvae and nymphs, and it would probably be correct to regard this species as a true island subspecies of *vieta*.

As *Schöngastia* appears to be an Old World genus, the list below includes the world species. Some of Lawrence's species are included provisionally because of the scutal shape and reptilian hosts, the question of the nude seta on tarsus III being *sub judice*. Five others African species are recorded from mammals. *S. andrei* Rad., *S. cercopithecii* (Trag.), and *S. willmanni* Rad., have the general appearances of this genus but their descriptions are lacking in a number of data. Fuller (1948) redescribes *cercopithecii* and notes the presence of mastitarsala III; Mr E. Browning of the British Museum (Natural History) has kindly examined *andrei* and *willmanni* and states that *andrei* has two mastitarsalae III and *willmanni* one. *S. lavoipierrei* Jadin and Vercammen-Grandjean, 1952:621, is a typical *Schöngastia* with one mastitarsala III. *S. oubanguiana* André 1951, also from mammals, has the characteristic scutum and toothed chelicers, but tarsus III is not described and the presence or absence of a mastitarsala III is uncertain; two sensory rods are mentioned and drawn for tarsus I but as the microtarsala is not noted, it may be that in this species the microtarsala I is exceptionally elongated. A detailed study of the legs would be interesting.

World Species.—Africa: *andrei*, *cercopithecii*, *platysauri*, *pseudocoryli*, *scincicola*, *willmanni*, probably *gerrhosauri*, *mabuyana*, *monticola*, *oubanguiana*. Asia and Pacific: *blestowei* (?), *philipi*, *pseudoschuffneri*, *schuffneri* N (= *pusilla*); *taylori*; *vandersandei* (? = *blestowei*); *vieta vieta* N & v. *maldiviensis* N (assuming provisionally that the latter is a geographic "island" subspecies, which appears likely); *whartoni*; "BP" n. sp., Varma in MS. Also *haddowi* Rad. 1953 (hyrax, Africa).

Genus *Oenoschöngastia* Womersley and Kohls, 1947

Type.—*Oenoschöngastia cana* Wom. & Kohls, 1947:8, *Trans. R. Soc. S. Aust.*, 71, 2-12. From nest of ground-bird, New Guinea.

Diagnosis.—Monotypic: larva similar to those of *Schöngastia* but chelicers differently modified (short, stout, curved and stumpy with several apical prongs). Nymph unknown.

Genus *Radfordiana* Womersley, 1953

Type.—*Radfordiana rostrata* Wom., 1952:242, *Rec. S. Aust. Mus.*, 10, 1-435. From soil, nest of ground-bird, and lizard, New Guinea.

Diagnosis.—Monotypic: larva similar to *Schöngastia* but chelicers differently modified (very long, serrated, almost styliiform); hypostome long, tongue-like, palpi long and slender, palpal claw a single prong; sensillary bases posterior to line of PLs.

Remarks.—In the general scutal shape, the presence of a mastitarsala III, and host-preferences (birds and reptiles) both *Oenoschöngastia* and *Radfordiana* are very close to *Schöngastia* s. str. The modification of the chelicers already present in *Schöngastia* appears to have been carried further in these two species. The writer believes it best to *think* of these two genera as being subgenera of *Schöngastia*.

Genus *Euschöngastia* Ewing, 1938, expanded

Type.—(*Euschöngastia americana* Ewing, 1938:293, *J. Wash. Acad. Sci.*, 28, 288-295, synonym) = *Schöngastia sciuricola* Ewing, 1925:261, *Amer. J. trop. Med.*, 5, 251-265. From squirrels, U.S.A.

Provisional Diagnosis (sensu lato, roughly equivalent to subgenus *Ascoschöngastia*, Wom. 1952:170).—Trombiculinids whose larvae have variously shaped scuta, 5 scutal setae and expanded sensillae (globose or lanceolate); legs usually 7-segmented but occasionally legs II and III 6-segmented; chelicers only

rarely serrated or with teeth; wide host range but mostly on mammals. Nymphs and Adults similar to those of *Schöngastia* but with eyes and precoxal plates absent or completely fused to form a sternum, in species so far examined.

Remarks.—As discussed in a footnote by Womersley (1952:170) and reaffirmed in a paper to be published (Womersley and Audy, 1955) *Euschöngastia* has priority over *Ascoschöngastia* and the former should be extended to include all those chiggers which have been included in *Schöngastia* (*Ascoschöngastia*) by Womersley (*loc. cit.*). Womersley's intention in this matter is quite clear (private communication), and evidently the amendment of his monograph proved impracticable.

The writer believes that *Schöngastia* sensu stricto discussed above is a valid genus. The assortment of chiggers included by Womersley in his subgenus *Ascoschöngastia* (amended to *Euschöngastia*) are therefore here treated as a genus, *Euschöngastia* sensu lato.

As noted below, however, the type (*E. sciuricola*) belongs to a species-group which has hitherto been distinguished by the accessory apical prongs to the palpal claws. Although the number of prongs on the claws is by itself a variable character of doubtful significance, this species-group appears to be distinctive in other ways and the writer doubts if such species as *E. lacunosa* (Gater) and *E. indica* (Hirst) will ultimately prove to be congeneric with it. Usage however dictates that *Euschöngastia* should for the time being taken as the temporary repository. As with *Trombicula* it appears to the writer that the proper procedure here is to attempt to define the type subgenus fairly strictly, and to recognise as many distinct species-groups and possible subgenera as may be necessary. A number of species will for a time inevitably remain unallocated to a group within the genus. As a step in the stabilisation of these affiliated groups, a new subgenus is here raised to accommodate the well-knit *lanius-mutabilis*-group. It will probably be helpful to raise another subgenus for the *indica*-group also, but this would at present be premature, because the *indica*-group might prove to be congeneric with *Doloisia*.

Subgenus **Euschöngastia** Ewing, 1938

Type.—(*Euschöngastia americana* Ewing, 1938: 293, *J. Wash. Acad. Sci.*, 28, 288-295, synonym) = *Schöngastia sciuricola* Ewing, 1925:261, *Amer. J. trop. Med.*, 5, 251-265. On American rodents.

Diagnosis.—Larvae with a characteristic shaped scutum, generally broader than long, with PW appreciably wider than AW and the posterior margin medially convex; palpal claws variable but generally with several small apical accessory prongs, 4-6 in number (these may vary in number even on both sides of the same specimen, and may be obscured by the main axis of the claw); so far not recovered from the Asiatic-Pacific area.

Remarks.—It might be a mistake to insist on the regular presence of the apical prongs on the palpal claws in the diagnosis of this subgenus. Certain African species appear to be related, but have 3-pronged claws. These are *aethomyia*, *otomyia*, and two species very near to these sent to the writer by Dr. Lawrence: the latter species have a mastitibiala and a mastitarsala III, both very fine and tapering, but the writer has been unable to compare them with any of the described species.

Subgenus **Helenicula** nov.

Type.—*Neoschöngastia lanus* Rad., 1946:261, *Proc. Zool. Soc. Lond.*, 116, 247-265. From a bird and rats, Indo-Burma border.

Diagnosis.—Larval *Euschöngastia* with shield-shaped scuta with convex posterior margins (cf. *Schöngastia* s.s., but emarginate in *signata*) and sensillary bases very close together (ca. 15 μ , or considerably less than twice the diameter of the bases, apart), globose sensillae, with basal stem; generally with multisetose coxae III (1-setose in *signata*); without mastitarsala III. Several species appear to be widely distributed and there is evidence suggesting that larvae of this subgenus are seasonal, appearing in relatively cold dry seasons. Nymphs & Adults (based on 4 species) with the general characters of *Euschöngastia* but with thickened and well-barbed shafts to the sensillae, a relatively narrow sensillary area (ASL/SB ratio 2.3-2.8). The posterior dorsal setae in *mutabilis* and *signata* have a long terminal setule. Not recorded from the New World.

Remarks.—This is the *globulare*-group in Womersley's Key (1952:231). The dry-seasonal appearance of larvae of this group has been noted elsewhere (Audy, 1947; 1953, table 4; Audy *et al.* 1953). The writer has pleasure in naming this subgenus for his mite of a daughter. A revision of the subgenus is to be published with the description of further nymphal material. The inclusion of the two African species listed below is subject to confirmation.

Old World species.—Africa: ?? *madecassa*; ? "SGH" n. sp. Jad. & Verc., 1953 in press. Asia and Pacific: *covelli*, *comata*, *globulare*, *kohlsi* N, *lanius* N, *miyagawai*, *mutabilis* N, *signata* (N unpub.).

Subgenus **Walchiella** Fuller, 1952, modified.

Type.—*Trombicula oudemansi* Walch, 1922:35, *Geneesk. Tijds. Ned. Ind.*, 62, 530-588. From mammals Malaysia and ?Australasia (type from Sumatra).

Provisional Diagnosis (expanded).—Larval *Euschöngastia* species close to those of the *lacunosa*-group (below) differing from them in having the femora of legs II & III undivided, these legs therefore 6-segmented instead of 7-segmented; chelicerae sometimes toothed or serrated, often simple, scutum well-chitinated and roughly rectangular but with posterior margin laterally rounded; bases of body-setae well-chitinated, generally conspicuous (DS set in platelets in *heaslipi*, *traubi*), setae often fairly short with inconspicuous barbules, and a general tendency for the DS to vary in length according to position; without a mastitarsala III. Nymphs & Adults (known only for *oudemansi* and n. sp. undescribed) apparently with fine nude sensillae (cf. *S. vieta*), sensillary area fairly broad relative to crista (ASL:SB ratio about 1.9); not clearly distinguishable from those of other groups of *Euschöngastia*. Not yet recorded outside Asiatic-Pacific area.

Remarks.—The type species, *E. oudemansi*, is a dominant chigger on ground-dwelling animals in the Malayan forest (see Table 1) and it can now be recognised as the dominant member of a considerable and widespread species-group. *E. oudemansi* itself has, as originally described by Walch, a row of distinct teeth and typical Malayan material shows these clearly [not as figured by Womersley, 1952, fig. 32C, which is probably the chelicer of *E. impar* (Gunther, 1939)] Dr. D. J. Lee of Sydney University has kindly allowed the writer to study a paratype of Gunther's *impar*, while Womersley has kindly lent a whole series of slides of material from New Guinea. From a study of these, it would appear that two distinct forms have been confused: one, *impar*, is without teeth to the chelicers (or perhaps with minute serrations ?) while the posterior dorsal-setae of the nymphs have very long subterminal setules; the other, typical *oudemansi*, has recognisable cheliceral teeth and the subterminal setules are relatively short. The scuta appear to be shaped somewhat differently. Whether or not these two forms (which may occur in the same locality) are two species or only varieties or subspecies now overlapping, the writer is not prepared to discuss. Until the material has been studied, it would be advisable to regard *impar* as a valid species, or at least as a distinct form.

E. oudemansi is a very small species, and in the small nymph the setation of the legs is simplified. This gives what may be false air of distinction to the chaetotaxy and it is hoped that a large species like some of those from Borneo may be bred in the near future.

Although the writer believes that *Walchiella* is probably a good larval genus, it is not possible to separate it generically from the *lacunosa*-group and until the two groups have been studied closely it would appear best to treat *Walchiella* as a sister group, i.e. as a subgenus.

World species (Asia & Pacific).—*asonluca* Traub & Audy, 1953 (this *Study* p. 84), *calunosa* Traub & Audy, 1953 (*ibid.*, p. 84), *heaslipi*, *impar*, *lewthwaitei*, *oudemansi*, *traubi*, 5 species being studied (one species bred to nymph).

Subgenus (?**Walchiella**): **lacunosa**-group

Representative Species.—*Neoschöngastia lacunosa* Gater, 1932:156, *Parasitology*, 24, 143-174. Common on ground-living rats in Malayan forest.

Provisional Diagnosis.—*Euschöngastia* species whose larvae differ from those of *Walchiella* in having all legs 7-segmented, but which otherwise share the following characters: scutum well-chitinated, punctate, roughly rectangular but PW often wider than AW; anterior and lateral margins nearly straight, posterior margin characteristically flattened or slightly concave medially and convexly rounded laterally towards the PLs; sensillae clavate to lanceolate; bases of body-setae well chitinated; a tendency for scutal and dorsal setae to vary considerably in relative length from species to species; without a mastitarsala III. Nymph described for only one species (*lacunosa*): a typical *Euschöngastia*. Not recorded from the New World.

Remarks.—Both the *oudemansi*- and the *lacunosa*-group are immediately recognisable by the general appearance of the scutum. There is a most convincing similarity which is difficult to convey by illustrations or words. There is wealth of material from Malaysia and Australasia and it is premature to discuss this group until further studies have been made. We need only note that it is exceptional for members of the *oudemansi*-group to have toothed chelicers, and that femora II and III are imperfectly divided in several members of the *lacunosa*-group. Therefore we either have an extraordinary close convergence in two different groups, or they are but one, and the *lacunosa*-group should be included in *Walchiella*, which may then be restored to generic rank.

World species (Asia & Pacific).—*lacunosa* NA, *plawrencei* (= *guntheri*), *nadchatrami* N, *phascogale sarawakensis*, *smithi*, *wongabelensis*, 4 n. spp. in MS.

? New subgenus: **indica**-group

Representative Species.—*Schöngastia indica* Hirst, 1915:187, *Bull. ent. Res.*, 6, 183-190. Common and widespread, especially on rodents (including house-rats) in Asiatic-Pacific area.

Provisional Diagnosis.—Species of *Euschöngastia* whose larvae have small subquadrate scuta, usually lightly chitinated, with AW 20-50 μ and AP 20-30 μ (?except in *rattus*, AP 42); AM in advance of ALs with the shoulders of the scutum rounded in front of ALs; AM longer than ALs; posterior scutal margin sinuous or slightly convex; sensillary bases about centrally placed, sensillae clavate with a basal stem, not globose; eyes present or absent; legs usually short with relatively thick, stumpy segments, frequently with one or more nude setae on tarsus III, body and leg setae usually delicately barbed or ciliated, not stout or plumose. Nymphs & Adults (described for *indica*, *audyi*) apparently not distinctive, of general *Euschöngastia* facies with ASL: SB ratio almost 2; sensillae hirsute, slightly thickened in *audyi*. N.B.: *debilis*, *labuanensis*, are exceptions noted below.

Remarks.—*Eusch. indica* is the dominant species infesting domestic rats in villages and towns from India to Malaysia and the Philippines; its range extends to Guam and New Guinea. In Malaya it is also a dominant species infesting tree-nesting rats in plantations and the forest-edge, but within the forest it is replaced by *audyi*, which was first collected in South Burma in 1945. *E. audyi* is red (*indica* being white) and it is a dominant chigger on arboreal mammals in the forests in Malaya and Borneo. Gispén (1950) has recovered pathogenic rickettsiae from *indica* in Java, and Traub *et al.* (1950) have recovered *R. tsutsugamushi* from a species from Malayan squirrels recorded as *indica* but subsequently described as *audyi* (see footnote, Traub and Audy, 1953, this *Study* p. 77). This is clearly an important group. A good deal of nymphal and new larval material is at hand and its study may allow the limits of this group to be defined. It is necessary to clarify the relationships between the *indica*-group as here defined and (a) the uncertain genera *Ascoschöngastia* and *Pseudoschöngastia* and (b) such species as *debilis* and *labuanensis*, and (c) the genus *Dolosisia* sensu lato. It is worth noting the extraordinarily close resemblance between *Trombicula munda* and *Euschöngastia indica*—they are very easily confused if the sensillae are missing: there has been a very close convergence of characters in the larvae of two genera. *E. labuanensis* is very close indeed to *E. roluis* Traub and Audy, 1953 (this *Study* p. 79), but (sensillae excluded) it differs from it no less than *T. munda* differs from *E. indica*. It is clearly necessary to be cautious and the present writer would prefer to leave *debilis* and *labuanensis* *sub judice*. In both, the AM seta is in line with or slightly behind the line of the ALs and the anterior scutal shoulder is lacking; in *labuanensis* the concave posterior margin suggests a possible relationship with such species as *E. andrei*. There may be confusing intermediate forms linking the *indica*-group to *Dolosisia* and there appear sound reasons for regarding *Ascoschöngastia* at least as a sister group.

The exceptional depth (AP 42 μ) of the scutum of *E. rattus* appears to be partly due to a fracture in the very poorly chitinated scutum, visible under the phase-contrast microscope in a paratype kindly lent to the writer by Womersley.

Old World species (Asia & Pacific).—*audyi* N (A unpub.), *daria* T. & A. (N unpub.), *indica* NA (= *cockingsi* N), *indicella* T. & A., *lorius*, *ocellifera* T. & A., *roluis* T. & A. (N unpub.), *rattus*, *soekaboemiensis*, 2 n. spp. unpub. (species with authors T. & A. are new species, this *Study* pp. 77-88).

Unallocated species of *Euschöngastia*

See comments to unallocated species of *Trombicula*, p. 148.

foliata-group: *foliata*, *mccullochi*, *pseudomys*, *uromys*.

?lappacea-group: *?cassiope*, *edwardsi*, *lappacea*, *?queenslandica*, *womersleyi*.

?mohri-group (? related to *lacunosa*-group): *crinita*, *mackerrasae*, *mohri*, *rectangulare*.

otomyia-group: *aethomyia*, *otomyia*, n. sp. CORU 3711.

raui-group: *raui*, *innisfailensis* (= *bushlandi* syn); n. sp. Wom. & Audy in MS.

?similis-group: *dasycerci*, *derricki*, *perameles*, *similis*.

Ungrouped species.—Europe: *?berlesei*. Africa: *africana*, *alticola*, *annulata*, *?bottegi*, *brevipalpis*, *capensis*, *causicola*, *gerrhosauri*, *kalaharica*, *laurenti*, *longispina*, *matoppoanus*, *monticola*, *ophicola*, *origensis*, *rhabdomyia*, *rhodesiensis*, *transvaalensis*, *tropidosauri*, *viperina*. Asia & Pacific: *antipodianum*, *bidentata*, *cairnsensis*, *coorongensis*, *echymipera*, *hirsti*, *ikaoensis*, *lipoxena*, *madagascariensis*, *melomys*, *peregrina*, *philippensis*, *samboni*, *samoensis*, *setosa*, *trichosuri*, *westraliense*. Also *schlugeri* Rad. 1953 (India), and *kitajimai*, F. & Ob. 1953.

Genus *Ascoschöngastia* Ewing, 1946

Type.—*Neoschöngastia malayensis* Gater, 1932:158, *Parasitology*, 24, 143-174. Apparently host-specific to the tree-living rat *Rattus canus* in Malaya.

Diagnosis.—Trombiculids with the characters of *Euschöngastia* whose larvae have the PL setae off the scutum. Nymph (of *malayensis*) an undistinguished *Euschöngastia*.

Remarks.—This group may be clearly separated from *Euschöngastia* sens. str. and it will doubtless accumulate related species around it—possibly even some with the PLs on the scutum. It would be consistent in this paper to treat it as a subgenus of *Euschöngastia* but the present writer would hesitate to interfere again with this group, which has suffered a lot of taxonomic indecision. The relationships of the *indica*-group (p. 154) and of *Pseudoschöngastia* to this genus should be particularly well studied. Nor should species be automatically placed in it only because they have expanded sensillae and PLs off the scutum.

Old World species.—Africa: *aethiopica*. Asia: *capillata*, *malayensis* N, *masta*, “NOV” n. sp. Wom. & Audy in MS.

Genus *Pseudoschöngastia* Lipovsky, 1951

Type.—*Pseudoschöngastia hungerfordi* Lipovsky, 1951:95, *J. Kansas ent. Soc.*, 24, 95-102. From small mammals in U.S.A.

Diagnosis.—Trombiculids with the characters of *Euschöngastia* whose larvae have PLs off the scutum and also legs II and III 6-segmented; so far all from the New World.

Remarks.—This group seems to bear the same kind of relationship to *Ascoschöngastia* as *Walchiella* bears to the *E. lacunosa* group. The writer believes that its affinities lie with *Euschöngastia* and not with any of the gahrlepiines (walchiines). He also believes that (a) its generic status requires more confirmation, but (b) it would be foolish to do anything but leave it as a genus at the present stage of fluidity in concepts. Opinions as to the relative value of characters such as displacement of the PL setae and the leg segmentation are almost entirely personal and have not yet been tested by time. The sister genus *Walchiella* is not related and has temporarily been accommodated as a subgenus of *Euschöngastia* because it is not properly separable from the *lacunosa*-group. The new Malayan species noted under *Ascoschöngastia* shows a very indistinct division of the femora of legs II and III in some specimens, and the present writer has not been impressed with this character while studying the *oudemansi*- and *lacunosa*-groups.

Genus *Neoschöngastia* Ewing, 1929

Type.—*Schöngastia americana* Hirst, 1921:37, *Ann. Mag. Nat. Hist.*, 17, 37-39. From various birds and a lizard, North and Central America.

Diagnosis (after Wharton & Hardcastle, 1946 and Womersley, 1952).—Trombiculines of the *Schöngastia* generic group with scutum submerged in the striated cuticle, sensillary areas usually below a transverse ridge; chelicers with only dorsal tooth and recurved ventral tooth; coxa III sometimes

multisetose; mastitarsala III sometimes present; apparently confined to birds. Nymphs (known for 4 species) with sensillary area striated and entire not raised between sensillary bases to form longitudinal ridges; sensillary area reniform, hilus anterior; sensillae variable, lanceolate or almost filiform; eyes absent; opisthosomal setae of two types, long and short.

Remarks.—There is a great range of variation in this genus, in such characters as the shape of scutum and sensilla, and the setation of the palps, galea, scuta, coxae, and body. As Wharton & Hardcastle point out, the three species *carveri*, *namrui*, and *riversi* are so distinctive that “each could conceivably be made the type of a monotypic genus... on morphological grounds”. One of the four nymphs known is that of the distinctive *carveri*. The extraordinary association of the submerged scutum with exclusive parasitisation of birds is striking, but we may note that *E. rectangulare* from a rat has the scutum likewise partly submerged. The scutal submergence might be one of those perplexing examples of convergence which seem to occur in the chiggers—e.g. the very close similarity between *T. munda* and *E. indica* with occur together on house-rats in Malaya. A group which parasitises birds is exposed in both larval and post-larval stages to a particularly interesting complex of environments and the intensive study of this genus will undoubtedly be as fascinating as it will be instructive. An important question is whether this genus is regularly nest-infesting, i.e. whether the post-larval stages infest the nests, as appears generally to be the case with *E. indica* for example.

Old World species.—Africa: *mirafra*. India & Malaysia: *gallinarum* N, *salmi*, *thomasi*. Pacific area: *americana solomonis* N?, *atollensis*, *backhousei*, *bougainvillensis*, *carveri* N, *dubia*, *egretta*, *gallinarum* N, *monticola* N?, *namrui*, *pauensis*, *posekanyai*, *retrocincta*, *riversi*, *strongi*, *yeomansi*; *asakawai*, *okumurai*.

Genus **Mackiena** Traub & Evans, 1950

Type.—*Mackiena empodiformis* Traub & Evans 1950:126, *J. Wash. Med. Sci.*, 40, 126-219, from a bird, North Burma.

Diagnosis.—With the characters of *Neoschöngastia* but with empodium expanded to sucker-like or pad-like terminal discs.

Remarks.—This genus is probably best thought of provisionally as a subgenus of *Neoschöngastia*. There is no reason to suppose that the modified empodium alone relates this species to *Riedlinia*.

Genus **Guntherana** Womersley & Heaslip, 1943

Type.—*Neoschöngastia kallipygos* Gunther, 1939:183, *Proc. Linn. Soc. N.S.W.*, 64, 73-96 (synonyms *N. callipygea* Gun., 1939, *N. bipygalis* Gun., 1939, *G. parana* Wom., 1944). From rats and marsupial rats, New Guinea.

Diagnosis.—Trombiculines of the *Schöngastia* generic group whose larvae have paired posterior dorsal plates bearing pairs of setae on each side (the plates may appear fused in unengorged larvae); body often slightly constricted medially; eyes present; without mastitarsala III. The only known larvae (of the type) hatch from eggs cemented to the fur of the hosts. Nymphs & Adults similar to those of *Euschöngastia* but with sensillary area relatively very wide (ASL/SB=about 1.1); shallow posterior angle; sensillae unexpanded with barbs or ciliations along entire length of shaft; without eyes; precoxal plates of coxa I well defined, separated (no true sternum); dorsal setae slender, tapering, ciliated.

Remarks.—There is some difference of opinion on the correct name for the type, which was described as *N. kallipygos*. Gunther's amendment to *N. bipygalis* (*nom nov.*, Gunther, 1939, *Proc. Linn. Soc. N.S.W.*, 64, 471-473) is not acceptable as it was made for no valid reason, as Gunther himself accepts in his recent check-list.

Gunther (1952:2) has raised a new family, Guntheraninae, to accommodate this genus. He does this on the strength of the accessory dorsal plates, and in particular on the extraordinary habit recorded by Gunther of the attachment of eggs of *G. kallipygos* to the fur of the host (as Womersley, 1952:246 points out, this requires a good deal of further investigation). The present writer is not sure that grounds yet exist for considering the differences to be subfamilial

and prefers not to accept the Guntheraninae. *G. parana* Wom., 1944, listed by Wharton & Fuller (1952:83), is considered by Womersley to be a synonym of the type; Womersley also records *kallipygos* as a *nomen nudum*, the type being *bipygalis*; but a *nomen nudum* has no validity and therefore cannot invalidate a given name.

The species *tindalei* and *translucens* are known only from the adult stage and should therefore be ascribed to this genus tentatively. It will be necessary in future to decide whether nymphs and adults uncorrelated with larvae are more closely related to *Guntherana* or to *Doloisia* (new subgenus)—at present the only character appears to be the more simple sensillae of the former. The ASL/SB ratio of *translucens* is about 1.5.

Old World species (Australasia).—*kallipygos*; ?*tindalei* N, ?*translucens* A (larva of last two unknown).

Genus *Doloisia* Oudemans, 1910, expanded

Type.—*Doloisia synoti* Ouds., 1910:87, *Ent. Ber., Amst.*, 3, 83-90. From a bat, Europe.

Provisional Diagnosis (expanded).—Larval trombiculines of the *Schöngastia* group with 7-segmented legs, a characteristic small scutum with PW much wider than AW, with a tendency to multisetose coxae reaching its highest development in the genotype (all coxae multisetose) but may be only coxae III multisetose (? this character exceptionally absent); palpal claw generally stout and peculiarly curved, usually 3-pronged, but may be 2-pronged; chelicer short, somewhat curved, with a single large recurved dorsal tooth which may be blunt; a tendency to have more than one pair of humeral setae; without long nude setae on legs. Nymphs & Adults (known only for three new species, new subgenus, and for *oculicola*; not known for the typical subgenus) with the general characters of *Euschöngastia* but with a broad sensillary area and short crista (ASL/SB ratio=0.7-1.2, instead of over 1.7) resembling the scutum of *Guntherana*; sensillae conspicuously branched (with spiculate shafts in a new species and *oculicola*, with thickened shaft in another new species undescribed).

Remarks.—The writer knows of only 3 species which resemble the type closely in all characters, namely *D. okabei* Sasa *et al.* 1952 from Japan, *D. brasiliensis* (Fonseca), and *Doloisia* sp.* Varma (in MS) from India. In addition, Radford's species *manipurensis* from India is obviously closely related although coxa I is unisetose. Of the latter species Womersley (1952:204) states his belief that *manipurensis* "might be placed in *Doloisia* Oudemans 1910 as suggested by Fuller, 1948, if that genus can be validly separated from *Schöngastia* when the adults become known" Womersley lays particular stress on the importance of adult characters and doubtless this emphasis is a useful corrective to the development of a classification based almost exclusively on larval characters. The present writer however agrees with a number of other authorities, in recognising that "larval" genera may be perfectly valid. With some new larval and nymphal material to hand it appears that *Doloisia* represents a quite distinct group of considerable complexity.

Subgenus *Doloisia* Oudemans, 1910

Type.—*Doloisia synoti* Ouds. 1910-87, *Ent. Ber. Amst.*, 3, 83-90. From a bat, Europe.

Provisional Diagnosis.—Scutum not heavily chitinised, with posterior margin almost straight or concave; AM seta advanced in front of AL's (so as to make scutum almost triangular or pentagonal), AM and/or AL setae may be nude or almost nude; coxae II and III multisetose, coxa I multisetose or unisetose.

Old World species (Asia).—"HA" n. sp. Varma; *manipurensis* (fig. 3; but see comments below); *okabei*, *synoti*; ? 2 n. spp. from Assam and North Burma (U.S.A. Typhus Commission coll.).

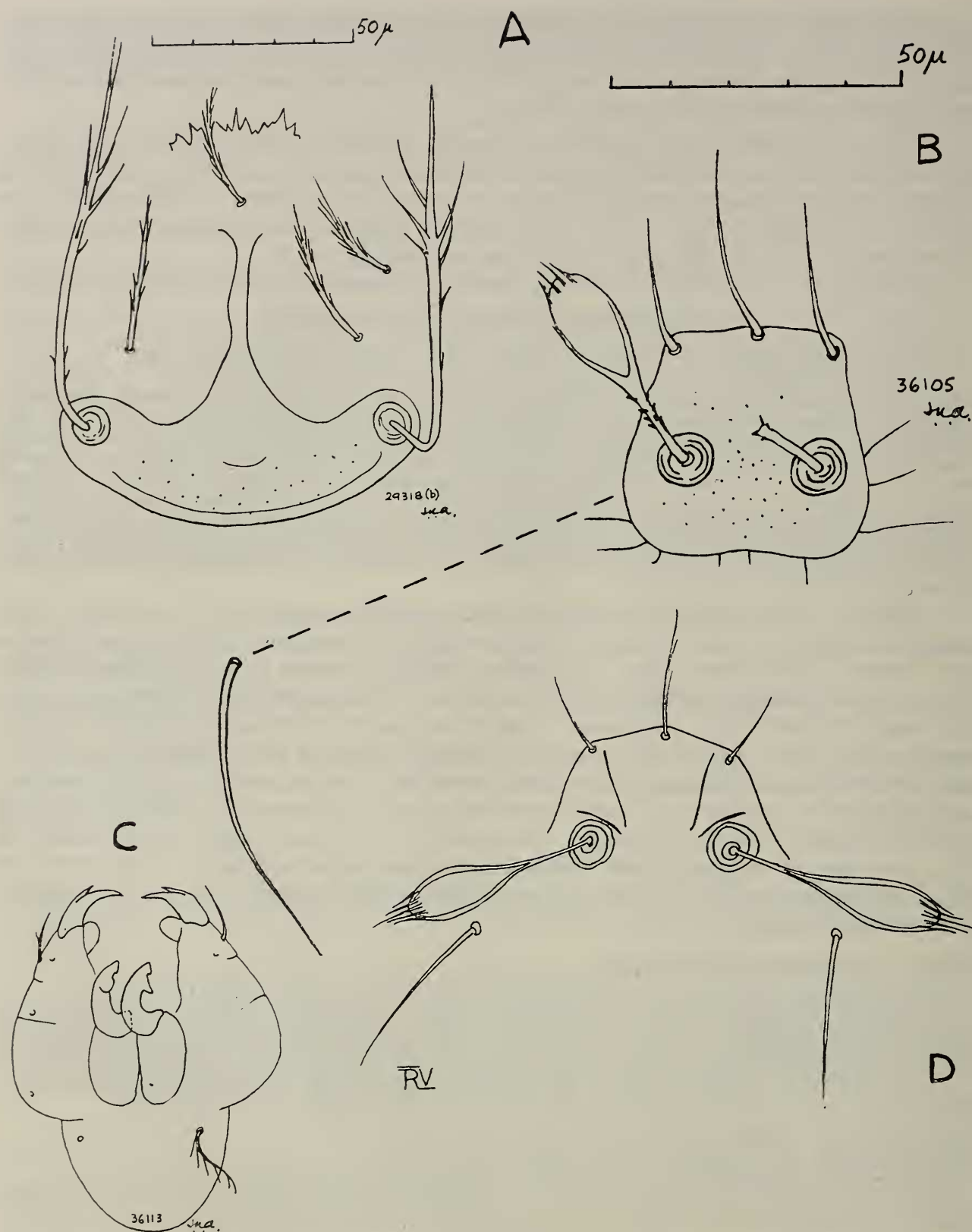
New Subgenus, "VN"-group Audy in MS (figs. 1, 3).

Type.—Malaysian species to be described and designated (Audy in MS).

Provisional Diagnosis.—With small scutum poorly chitinised; PL setae off the scutum and separating widely with engorgement; only coxae II and III multisetose. Nymphs & Adults as described in diagnosis of genus.

Remarks.—We have 4 species from Malaya and one (?two) from North Borneo which have the general characters of *Doloisia* except that the poor chitinisation of the scutum combined

* Since this went to press, Raja Varma has kindly allowed the writer to see his descriptions and illustrations. His new species (here listed as "HA") is close to *manipurensis* and both these species will probably prove to belong to the VN-group which is to be made a new subgenus by the present writer.



3. Characters of *Doloisia* sensu lato

A, scutum of Nymph, species "BL" in VN-group ; for comparison with the closely related species "VN" in fig. 1 on p. 129.

B, Scutum, and C, gnathosome (reduced scale) of species "VA".

D, scutum of *D. manipurensis* (Rad.) drawn by M. G. Raja Varma and reproduced with his kind permission, to same scale as B.

with the apparently slight posterior development seen in the typical group has led to a separation of the PLs from the scutum. Both specimens of the first species seen ("VN") were badly distorted but the resemblance to *manipurensis* was very close indeed, except that no scutal margins could be seen even with phase-contrast microscopy. Nymphs were available and proved sufficiently distinctive (fig. 1) to suggest that the species was generically well defined. A second nymph ("VA" new species, fig. 3) was identified as another *Doloisia* although it had been put aside as *?mutabilis* on account of a multisetose coxa III in the fragmentary larval pelt. A satisfactory description of this larva cannot yet be given. Two other species have recently been collected together (from a different locality, Fraser's Hill), in which the scutal character is obvious. The discovery of these has allowed us to decide that the original species "VN near *manipurensis*" (distorted specimens) also has PLs off the scutum. Mr. Raja Varma, Research Fellow of the Indian Council of Medical Research, has examined type material in the British Museum (Natural History) and has very kindly allowed his drawings of the scutum of *D. manipurensis* to be reproduced here (fig. 3c). Mr. Varma could not see the posterolateral and posterior margins, but this may be extremely difficult in an old mount. Nevertheless, the scutum is very poorly chitinised and the obviously close relationship between *manipurensis* and "VN" n. sp. requires further study—it is possible that *manipurensis* belongs to this new subgenus and not to subg. *Doloisia*, the completion of the indistinct scutum to the PLs in the original description having been due to a misinterpretation. Since this *Study* went to press another new species in this subgenus has been collected from moss forest near Mt. Trus Madi in North Borneo by the third joint Anglo-American expedition in July, 1953. This was a large species occurring within the nasal cavities of rats, a peculiar habitat already explored by P. H. Vercammen-Grandjean in the Belgian Congo (in a private communication Vercammen-Grandjean has commented on, and kindly sent the writer specimens of, new genera and species of intranasal chiggers: the credit for drawing attention to this habitat for chiggers belongs to him). The most significant feature of this new species is the absence of the strong curvature of the palpal claws, which are ordinary in appearance. This point is important when considering the possible relationships of several other species. The nymph, bred by Mr. Nadchatram, is closely similar to the others but the sensillae are more simply barbed. (Note: the intranasal habitat has been described by Wolf and Verc., 1953).

Old World species (Malaysia).—These are to be described in the next *Study* in this series. The species are listed below. It is interesting to note that the first 4 species all came from *Rattus bowersi* from two localities.

1. "VN" n. sp. N., Ulu Langat F.R., Selangor (Nymph, fig. 1).
2. "BL" n. sp. N. One nymph; incomplete larval pelt without scutum, provisionally included in this subgenus. From same host-species and locality as "VN" (Nymph, fig. 3)
3. "VA" n. sp. engorged larvae, from *R. bowersi*: Fraser's Hill, Pahang (fig. 3).
4. "ND" n. sp. engorged larvae, same host species and locality as "VA".
5. "NS" n. sp. engorged larvae, intranasal in rats, Mt. Trus Madi (Ulu Kaingaran), North Borneo; nymphs may shortly be available for study.

New Subgenus: **oculicola**-group **crocidura**-group

Remarks.—The writer is not prepared to give even a provisional diagnosis of this group or these groups without further study. There are probably several species already known which are more closely related to this group than to any other. *S.(S.) oculicola* Wom. (1952:167,383: plates 31, 103) has a small scutum similar to that of typical *Doloisia* except that the posterior margin is medially slightly convex and the SBs relatively somewhat close together. The strong 3-pronged curved palpal claw, the short modified chelicer (blunt denticulations replacing the large blunt tooth) and the additional humeral setae are also collectively important in relating this species to *Doloisia* rather than any species-group of *Euschöngastia*. In addition, the

distinctive nymph resembles those of "VN" and "BL" in shape (ASL/SB ratio about 1.2?) and in the sensillae having sparse long branchlets and spiculate shaft; the long, solitary, paracristal setae are however peculiar. Mr. Womersley is kindly providing material for further study. The peculiar location (conjunctiva) of *oculicola* on the host is interesting in view of the occurrence of "NS" n. sp. on the intranasal mucosa. One of Vercammen's species noted below was also intranasal. It must however be admitted that Vercammen has shown that a number of unrelated species favour this peculiar habitat.

The relationships of at least four other species to this group require study: *E. andrei* (Jadin and Verc., 1952:622), *E. crocidura* (Law. 1949) "DBI-NB" n. sp. Jadin and Verc. (1953 in press) and *E. nausheraensis* (Wom. 1952:202). A specimen of the third was very kindly sent to the writer by Vercammen-Grandjean of the Laboratoire Medicale Province du Kivu, Bukavu (Belgian Congo). It has a small scutum similar in shape to that of *E. andrei*, the 3-pronged palpal claws are characteristically curved terminally, the chelicers have the single large tooth, and coxa III is multisetose. *E. crocidura* is closely similar. This species may link *E. andrei* to the group under discussion. Womersley's species *nausheraensis*, of which the writer has kindly been lent several specimens, has a somewhat different scutum (larger, PW more nearly equal to AW, SBs relatively wide apart) but the posterior border is concave and the scutum generally resembles that of *andrei* (in this, Womersley's figure 52C is slightly inaccurate). There are only 2 humeral setae but coxa III is multisetose. The palpal claw is 2-pronged and not particularly short or incurved, resembling that of "NS" n. sp. from Borneo. Vercammen's species are in a number of features intermediate between *nausheraensis* and *oculicola*, and a good deal of study will be necessary to clarify these interesting relationships. *T. praomyia* Rad. from Africa and *T. jubbulporensis* Wom. have a peculiar scutum like those of *E. andrei* and *E. nausheraensis*: they have been described as *Trombicula* in the absence of sensillae and their true relationships are unknown.

Old World species, relationships sub-judice.—Africa: ?*andrei*, ?*crocidura*, "DBI-NB" Jad. & Verc. ?*dutoiti*. Asia: *nausheraensis*, *oculicola*.

Genus **Riedlinia** Oudemans, 1914

Type.—*Riedlinia coeca* Ouds. 1914:88, *Ent. Ber. Amst.* 4, 84-49. From a bat, hills near Bombay, India.

Diagnosis.—Monotypic: larva with spatulate empodium, claws stronger than usual; eyes absent; scutum roughly pentagonal, with posterior angle, sensillae unknown. Nymphs not known.

Remarks.—Womersley describes this species as having globose sensillae but Fuller (1952:200) in a redescription states that the nature of these organs is unknown. Kalra is attempting to collect topotypic material (personal communication). There is a *lapsus calamae* in Wharton and Fuller where the locality is given as Malaya.

Genus **Endotrombicula** Ewing, 1931

Type.—*Endotrombicula penetrans* Ewing, 1931:16, *Proc. U.S. Nat. Mus.*, 80, 1-19. From amphibian, East Africa.

Diagnosis.—Trombiculines with expanded sensillae, chelicers with large recurved teeth increasing in size proximally; apparently confined to amphibians.

Subgenus **Endotrombicula**, Wharton and Fuller, 1952

Type.—*Endotrombicula penetrans* Ewing, 1931:16. From amphibian, East Africa.

Diagnosis.—*Endotrombicula* whose larvae have a single tarsala I.

Old World species (Africa).—*madagascariensis*; *penetrans*; *pillersi*.

Subgenus **Phrynacarus** Lawrence, 1949, Wharton and Fuller, 1952

Type.—*Phrynacarus fitzsimonsi* Lawrence, 1949:463, *Ann. Natal. Mus.*, 11, 405-486. From amphibian, South Africa.

Diagnosis.—Monotypic; *Endotrombicula* whose larva has several (4) tarsalae I.

Subfamily GAHRLIEPIINAE Womersley

=WALCHIIINAE Ewing

Diagnosis (as in Womersley, 1952:278; as in Wharton and Fuller, 1952:91 but excluding genera *Walchiella* and *Pseudoschöngastia* which are here placed in the Trombiculinae).—Trombiculids whose larvae have no anteromedian or submedian setae on the scutum; scutum frequently extending backwards with or without inclusion of dorsal setae; expanded sensillae; leg I 7-segmented, legs II and III 6-segmented; coxa III frequently with two or more setae; no mastitarsala or mastitibiala III. Nymphs and Adults similar to those of *Guntherana* and *Doloisia* (new subgenus, above), with anterior rod of crista shorter than distance between sensillary bases; sensillae barbed along almost whole length; tarsus I with a subapical dorsal stump-like papilla; tectum rounded or conical, finely denticulate.

Remarks.—Out of a total of 53 larval species known to the writer, at least 20 have been correlated with their nymphs. On the basis of the close similarity between nymphs, Womersley has reduced the four known genera to subgenera of *Gahrlepieia* sens. lat. Previous to this, Womersley and Heaslip (1943:136) had synonymised *Schöngastiella* and *Gateria* with *Gahrlepieia* on larval characters. Gahrlepieine material from Burma, Malaysia, and Africa is being studied in detail by Traub, who is also in favour of recognising the broad genus until further studies clarify matters (Traub and Evans, T. and Morrow). An important contribution is being made by Vercammen who has discovered true gahrlepieine larvae with toothed chelicers in the Belgian Congo and has bred them to the nymph—the nymphs appear to be typical gahrlepieines (Vercammen 1953, and personal communication).

All these and also other workers are aware of the artificial nature of most of the divisions made between the present genera. In effect, these divisions have been made in steps according to the number of setae on the scuta until larvae with many and variable numbers of setae have made further efforts unprofitable; a division has then been made on the marginal or non-marginal placing of the setae on the scutum. The position therefore is that four generic divisions of dubious validity have been reduced to four subgeneric divisions which are still doubtfully valid, pending a revision to be made on the basis of more detailed study of larval and nymphal material. The first step in this revision would be to ignore the existing subgenera completely and to attempt to rearrange the assemblage of known species in natural groups. The following groups suggest themselves to the writer but this grouping is emphatically tentative and its object is simply to stimulate thinking away from the established subgenera. This particular rearrangement is largely based on the scuta, but much more attention should be paid to the chaetotaxy of palps and legs, to distribution of species on hosts and in space. The presence or absence of eyes has been considered of importance but this now appears to be of limited value. The writer himself suspects that more than one valid larval genus will emerge from the temporary repository of the broad genus *Gahrlepieia*, in which case it is possible that the old family name (Walchiinae) may be restored.

(1) **pingue-group**, comprising (A) *pingue*-subgroup, with *brennani*, *enode*, *disparunguis*, *lewthwaitei*, *morobensis*, *pingue*, and (B) *rioi*-subgroup, with *americana*, *rioi*, and n. sp. nr *rioi*. Members of subgroup A show some tendency to a posterior prolongation of the scutum, so that these species might in fact form a series with the *turmalis*-subgroup (below) in which a distinct narrow tongue is developed. Similarly, members of subgroup B may either be grouped with those of A, or they may be taken to form the first of the *bengalensis*-series, in having the posterior margin broader and more evenly rounded (in a new species near *rioi* from Selangor, this margin is very much convex).

(2) **turmalis-ligula-group**, comprising (A) *turmalis*-subgroup (*Walchia*) with *rustica*, *turmalis*, and n. gen. n. sp. Vercammen 1953 (in press), in which there is a distinct prolongation of the scutum to form a narrow tongue, while the chelicers show a tendency to develop a tooth or (in Vercammen's species) teeth. The position of Vercammen's species, including another mentioned below, is complicated by the fact that these two species have been obtained from

an unique locus on the host. The presence of teeth in these two species may be related to a special feeding requirement; it is thus either a convergent development in two different groups or it is a special adaptation of a single group. (B) *ligula*-subgroup (*Schöngastiella*) with *ceylonica*, *kalrata* Traub and Evans 1953 (this *Study* pp. 98, 99), *ligula*, *liota* T. & E., in which the tongue carries an extra pair of posterior setae, presumably derived from the dorsal setae, placed marginally and subterminally.

(3) **bengalensis**-group (*Schöngastiella*) comprising *bengalensis*, *brevis*, *coeca*, *dureni*, *erula*, T. & E., *helata* T. & E., *hipposideros*, *phomunguis*, *gammonsi* T. & E., *kumaonensis*, n. sp. CORU. R17506, plus three atypical members: *arona* T. & E. and *birella* T. & E. (which have the anus borne on a plate and a peculiar arrangement of dorsal setae; see this *Study* pp. 95, 96, 97), and possibly *saduski* (which to the writer appears to be a member of the *bengalensis*-group with a few extra setae on the scutum, variable in number). The possible relation of *G. nanus* to this group is noted below.

(4) **decora**-group (= *Gahrlepiea* in part), with *decora*, *insigne*, *ornata*, four related species from Malaysia and Burma with honeycombed scuta, and *cestrata*. Mr M. Nadchatram in studying a series of freshly mounted *G. cestrata*, noted that the punctuation of the scutum was of two kinds, the ordinary small punctae and also a number of large pits which gave a fenestrated appearance to the scutum. These pits or small fenestrae appear to represent the obvious honeycombing which reaches its full development in the other members of this group. It will be noted that this group in fact comprises the subgenus *Gahrlepiea*, with the possible exception of *nanus* the genotype, which the writer has not examined. According to Fuller (1952:213), the type has been excessively cleared, so that the detection of unusual punctuation would require a phase-contrast microscope and may no longer be possible. In any case, it would appear that *nanus* may either belong to the *cestrata*-*decora* group, which would then become sufficiently distinctive to be recognised as a genus; or *nanus* may be placed with *saduski*, in the *bengalensis*-group, in which case it might become necessary to synonymise *Schöngastiella* with *Gahrlepiea* and raise a new name for the *decora*-group. The coxae III in members of this group are remarkably deep. This character is present to a lesser extent in the *bengalensis*-group but not in the *ligula*-group. Womersley (1952:301) includes *saduski* in the subgenus *Gahrlepiea* although some of the setae are not marginal: it is either a *Gateria* or a member of the *bengalensis*-group as noted above.

(5) **fletcheri**-group (= *Gateria*), with *ciliata*, *crocidura*, *fletcheri*, *hirsuta*, *lancearia*, *longipili*, *rutila*, ?*saduski*, *spinulosa*. Fuller (1952:217) notes that *crocidura* and *lancearia* cannot at present be properly distinguished. The relationship between the *bengalensis*-group and the *fletcheri*-group requires careful study: it might be a mistake to draw a line between the two simply on scutal setal counts.

(6) **longiscutullata**-group (*Giroudia* Jad. & Verc.), with two African species *Giroudia longiscutullata* and *G. brennani*. These have the characters of *Gateria* but also have teeth on the chelicers.

Type species.—In view of these uncertainties, the writer prefers not to list and give diagnoses for either the accepted or the tenuously tentative subgenera/genera. A list of the type species is given for reference, and the appended list of Old World species simply follows the accepted classification.

Gahrlepiea Oudemans, 1912:273, *Ent. Ber. Amst.*, 3, 272-278. Type *Typhlothrombidium nanus* Ouds., 1910:105, *idem*, 3, 103-109. From a bat, South Africa.

Schöngastiella Hirst, 1915-188, *Bull. ent. Res.*, 6, 183-190. Type *Schöngastiella bengalensis* Hirst, 1915-188, *idem*. From rats, India.

Walchia Ewing, 1931:11, *Proc. U.S. nat. Mus.*, 80, 1-19. Type (*Thrombidium glabrum* Walch, 1927:926, *Geneesk. Tijd. Ned-Ind.* 67, 922-933, homonym, not *Thrombidium glabrum* Duges) = *Walchia pingue* Gater, 1932:173, *Parasitology*, 24, 143-174. From rats, Indo-Malaysia.

Gateria Ewing, 1938:295, *J. Wash. Acad. Sci.*, 28, 288-295. Type *Gahrlepiea fletcheri* Gater, 1932:161, *loc. cit.* From rodents & insectivores, Malaya.

Old World species.—Africa: *Schöngastiella coeca*; *Gahrlepieia lawrencei*, *nana*, ? n. sp. CORU 36695 sent by Dr. Lawrence from South Africa; *Giroudia brennani*, *longiscutullata*. *Gateria philipi*, N. g. n. sp. Vercammen, 1953 in press N. Asia &c.: *Walchia brennani* N, *disparunguis* N, *enode* N, *lawrencei* N, *morobensis* N, *ogati*, *pingue* N, *rioi*, n. sp. nr. *rioi*, *rustica* N, *turmalis* N. *Schöngastiella arona* T. & E. N, *bengalensis* N, *birella* T. & E., *brevis*, *ceylonica* N, *erula* T. & E., *gammonsi* T. & E., *helata* T. & E., *hipposideros*, *kalrata* T. & E., *ligula* N, *liota* T. & E., *punctata* N., *SIN* n. sp. (Varma in litt.), n. sp. CORU in MS. *Gahrlepieia cetrata* N, *decora*, *insigne*, *ornata* N, 4 n. spp. in MS. *Gateria romeri*, *rutila* N, *spinulosa*. Also *Sch. wansoni* Wolfs & Verc. 1953 from Africa.

FAMILY LEEUWENHOEKIIDAE WOMERSLEY

OR Subfamilies LEEUWENHOEKIINAE Womersley

and APOLONIINAE Wharton

Provisional Diagnosis of Tentative Family (after Womersley, 1945; Wharton & Fuller 1952:90, 96; Baker & Wharton, 1952; Womersley, 1953, this *Study* p. 108; also Brennan, Wharton, and Womersley, personal communications), for comparison with diagnoses of Trombiculidae & Trombidiidae, pp. 137, 166 Larvae so far known with only one dorsal plate (the scutum) usually carrying an anterior median process (nasus): always with only one pair of sensillae, usually filiform sometimes expanded (when filiform usually nude). Six scutal setae, 2 antero-submedian (except in 2 new genera Wom., 1953), 2 anterolateral, and 2 posterolateral; seta on pedipalpal coxa posterior to base of palpal femur; cheliceral blade frequently modified (toothed, with or without modification of the blade); femora of all legs, or of legs II and III undivided (except in Apoloniinae) and these legs therefore 6-segmented; coxa I 2-setose (except in *Chatia* & *Womersia*), coxa III 1-setose (multisetose in *Chatia*); parasitic on arthropods and vertebrates. Stigmata and tracheae may be present (*Acomatacarus*, *Whartonia*). Nymphs and Adults mostly small (1-2 mm or less), body cordate or pyriform, not constricted (except in *Hannemania*). Scutum with one pair of filamentous sensillae arising from a subposterior sensillary area; scutum ending anteriorly in a triangular tectum usually bearing a pair of setae. Eyes if present 2+2, sessile, away from scutum. Dorsal setae frequently of two kinds.

Remarks.—Few leeuwenhoekiiids have been encountered in India and Malaysia and the present writer is not familiar with the group. He is not prepared to offer any opinions as to the familial or other status of the Leeuwenhoekidae or its components. An attempt is here made to tabulate the known facts and to present a tentative diagnosis of the families Trombiculidae, Leeuwenhoekidae, and Trombidiidae partly for reasons already noted but largely for the writer's own edification.

Most species of this family are known from the larvae. Of the 88 known species (including some of the undescribed species, Womersley in MS, personal communication), 50 are of species of *Acomatacarus* parasitising vertebrates and 16 are species of *Hannemania* from batrachians. Of the ?12 known nymphs and adults 8 are of *Acomatacarus*. The adults so far known are therefore not representative. Womersley is completing a monograph of this family. In the species-lists which follow Wharton & Fuller are followed but the Apoloniinae are provisionally extended after Womersley's revision (1953).

Subfamily LEEUWENHOEKIINAE Womersley

Provisional Diagnosis (Wharton & Fuller, 1952:96, *verbatim*).—"Trombiculids whose larvae have two setae on coxae I, all legs composed of six segments and attenuated sensillae."

Remarks.—Three genera are not represented in the Old World; they are however included in the Table. *Chatia* Brennan in monotypic. Dr. Brennan has very kindly allowed his comments on the nymphs to be quoted (letter of March 1953): they have "no constriction between proterosoma and hysterosoma...pyriform rather than cordate...they have very long legs and are quite similar to *Acomatacarus* nymphs." The nymphs are being described by Lipovsky. *Odontacarus* Ewing, according to Wharton & Fuller (1952:103) is probably a synonym of the subgenus *Acomatacarus*: the specimens in existence are too badly damaged to be studied satisfactorily. *Leeuwenhoekia* Ouds. s. str. is represented by two species from mammals in the Americas: *L. (L.) verduni* (Ouds), and *L. (Comatacarus) americanus* (Ew).

Brennan (1949) and Wharton (1950) have made careful studies of the respiratory organs of chiggers and Wharton & Fuller (1952 : 28) have summarised information up to date. Salivary ducts with taenidia may easily be, and have been, confused with true tracheae in chiggers. A system of unbranched taenidia (opening on a pair of spiracles or stigmata between coxae I and the gnathobase) is apparently truly respiratory and is "characteristic of certain species of the genera *Acomatacarus* and *Whartonia*." The salivary ducts with taenidia have been seen in various genera including *Neoschöngastia*.

Genus *Acomatacarus* Ewing, 1942

Type.—*Acomatacarus arizonensis* Ewing, 1942:490, *J. Parasit.*, 28, 485-493. From reptiles, Mexico and U.S.A.

Diagnosis (Wharton & Fuller, *verbatim*).—"Leeuwenhoekiiids whose larvae have an anterior, median scutal projection, paired submedian scutal setae, and a series of teeth on a relatively modified cheliceral blade" Nymphs & Adults (known only for subgenus *Acomatacarus*) not constricted.

Remarks.—The following list includes the four subgenera represented in the Old World, viz. *Acomatacarus* Ew., *Hyracarus* Law., *Austracarus* Law., and *Austrombicula* Law., without repeating their diagnoses. The writer is grateful to Womersley for information about those species which have been bred to the nymph, and for details of unpublished species.

Old World species.—Europe: *paradoxus*. Africa: *A. (Acom.) gateri*, *geckobius*, *jaegerskioldii*, *lacertae*, *mabuyana*, *namaquensis*, *tenuitarsus*, *thallomyia*, *?theileri*. *A. (Austracarus) procaviae*, *polydiscum*. *A. (Austrombicula) womersleyi*. *A. (Hyr.) typicus*, *lawrencei*, *longipilosus*, *natalensis*. Asia and Pacific: *A. (Acom.) adelaidae*, *athertonensis*, *atollensis*, *attolus* A., *audyi*, *australiensis*, *?barrinensis*, *dromus*, *echidnus*, *?gymnodactyli* (Ew.), *longipes*, *lygosomae*, *mccullochi*, *nova-guinea* N., *patrius* A., *retentus* A., *southcotti*, and over 7 n. spp. (incl. 2 with nymphs) Wom. in MS.; *yosanoi* F. & Ob., 1953.

Genus *Hannemania* Oudemans, 1911

Type.—*Heterothrombidium hylodeus* Oudemans, 1910:88, *Ent. Ber.*, *Amst.*, 3, 83-90. From skin of an amphibian, Brazil.

Diagnosis (from information provided by Wharton).—Leeuwenhoekiiines whose larvae have an anterior medial scutal projection; without stigmata or tracheae, but with well-developed salivary ducts; well-developed teeth disrupting the blade-like conformation of the chelicera; apparently confined to amphibia, penetrating the skin. Nymphs & Adults distinguished by having constricted bodies ("figure-8"). Mostly recorded from the New World.

Remarks.—The nasus to the scutum has been missed in some species (e. g. *H. hylodeus*, *rouxi*—see Fuller 1952 : 239) and as a result this genus has accumulated some species properly belonging to *Whartonia* (q. v.). Ewing (1926) illustrated the constricted nymph of *H. hylae* and Wharton (letter dated April 1953) states that "at least four species of *Hannemania* have been reared and all have the 8-shaped nymphs and adults."

Old World species.—Europe (Sweden): *Hannemania* sp. Sellnick, 1949:129, *Ent. Tidskr.*, 70, 123-135. Pacific (New Caledonia): *rouxi*.

Genus *Whartonia* Ewing, 1944

Type.—*Hannemania nudosetosa* Wharton, 1938:142, *Carn. Inst. Wash. Publ.*, 491, 137-152. From bats, Mexico.

Diagnosis (after Wharton & Fuller, and Wharton in a letter of April, 1953).—Leeuwenhoekiiines whose larvae are without an anteromedian projection (nasus) to the scutum; cheliceral blades modified as a series of recurved teeth; with spiracles (stigmata) and tracheae (cf. *Acomatacarus*): apparently confined to bats. Nymphs and Adults, according to Wharton in correspondence, known for "*Whartonia nudosetosa* and two other species," which have "cordiform nymphs similar to *Acomatacarus*, whose larvae also have spiracles and tracheae."

Remarks.—*Hannemania perplexa* Bren. and the *Hannemania* n. sp. from Malaya noted by Audy (1952) both belong to *Whartonia*. Four species seen by the writer are very large chiggers.

Old World species.—Africa: 2 n. spp. from bats in the Sudan sent by Dr. Thompson to Dr. Zumpt. Asia and Pacific: *vellae*; 1 n. sp. Wom. in MS from Malaya; 2 n. spp. from Borneo.

SUMMARY OF CHIEF CHARACTERS

GENERA AND SUBGENERA OF LEEUWENHOEKIINAE AND APOLONIINAE.

Genus (Subgenus).	Larvae Nymphs Adults known.	LEGS.		SCUTUM.			CHELICERS.		Hosts.	Remarks.
		No. segments I:I:III.	Coxal setae I:II:III.	Nasus present.	Setae AM: AL:PL.	Sensillae.	Dorsal, ventral rows teeth.			
<i>Leeuwenhoekia</i> Ouds.	L	6:6:6	2:1:1	Small ...	2:2:2	filamentous	only usual cap	...	M, America	pentag. scutum; nude setae tib. and tarsus III.
(<i>Leeuwenhoekia</i> Ouds.)	L	do.	do.	do.	do.	do.	do.	...	do.	without spiracles and tracheae.
(<i>Comatacarus</i> Ew.)	L	do.	do.	do.	do.	do.	simple row	...	M, B, R	pentag. scutum.
<i>Acomatacarus</i> Ew.	LNA	do.	do.	do.	do.	do.	do.	...	M, B, R	with spiracles and tracheae.
(<i>Acomatacarus</i> Ew.)	LNA	do.	do.	do.	do.	do.	do.	...	M, Africa	without sp. and trach.
(<i>Austracarus</i> Law.)	L	do.	do.	do.	do.	do.	do.	...	M, Africa	without sp. and trach.
(<i>Austrorbicula</i> Law.)	L	do.	do.	do.	do.	do.	do.	...	M, R, Africa	without sp. and trach.
(<i>Hycarus</i> Law.)	L	do.	do.	do.	do.	do.	d, v, medial	...	M, R, Africa	with spiracles and tracheae.
(<i>Xenacarus</i> Greenberg)	L	do.	do.	do.	do.	do.	do.	...	M, America	without sp. and trach; without empodium; palpal claws about 7 prongs.
<i>Chatia</i> Bren.	LN	do.	2:1:5-7	Absent...	do.	do.	none	...	M, America	
<i>Shusennia</i>	L	do.	2:1:1	Absent...	do.	do.	small subapical, d	...	M, Korea, America	without sp. and trach; empodium present; palpal claw 3-4 pronged.
Jameson and Toshioka	LNA	do.	do.	Small ...	do.	do.	blade disrupted	...	Amphibia	without sp. and trach; ? with nude setae tib. and tarsus II; constricted nymphs.
<i>Odontacarus</i> Ew.	L	do.	do.	Small ...	1:2:2	do.	simple row	...	M, America	with sp. and trach.
<i>Whartonia</i> Torr. and Brag	LN	do.	do.	Absent ...	2:2:2	do.	recurved	...	Bats	with sp. and trach.
<i>Apolonia</i> Torr. and Brag	L	7:7:7	1:1:1	Large ...	2:2:0	do.	none	...	B, America	saliv. ducts +; small scutum.
<i>Sauracarella</i> Law.	L	do.	1:1(2):1	Small ...	2:2:2	globose	none	...	R, Africa	saliv. ducts poor.
<i>Womersia</i> Wharton	L	do.	1:1:1	Large ...	1:2:0	fil.	none	...	B, America	saliv. ducts +; small scutum.
<i>Womersleyia</i> Rad.	L	do.	—	Small ...	2:2:2	do.	none	...	A, Indian atoll	
<i>Grossia</i> Wom.	L	do.	2:1:1	Absent...	0:2:2	do. barbed...	d, v, (fine)	...	A, Australia	4-hooked palpal claws, no empodium; peculiar setae base tarsal claw.
<i>Neotrombidium</i> Hirst	LA	do.	2:1:2	Large ...	2:2:2	fil.	none	...	Australia; and Bats America.	hooked palpal claws: single tarsal claw.
<i>Nothotrombicula</i> Dumb.	L	do.	2:1:1	Medium	1:2:2	fil.	short	...	A, Australia	hooked palpal claws; no empodium.
<i>Audyana</i> Wom. 1953	LN	7:6:6	peglike 2:1:1	Absent...	2:2:2	slender fusiform	2 small subapical hooklike	...	A, Malaya	
<i>Cockinesia</i> Wom. 1953	L	do.	2:1:1	Small ...	peglike do.	fil.	none	...	A, Malaya	single tarsal claw, no empodium.
<i>Mackerrastella</i> Wom. 1953	L	do.	1:0:1	Medium	do.	do. barbed	none; hooklike	...	A, Australia	no sternal setae.

* The nymph now allows this genus to be placed in the Trombididae, Trombellinae.

Subfamily APOLONIINAE Wharton

Provisional Diagnosis (Wharton, 1947, slightly simplified to include new genera tentatively introduced by Womersley, 1953, this *Study* p. 108).—Leeuwenhoeikiids with 7-segmented legs (except for *Cockingsia*); sensillae expanded or attenuated; mostly parasitising reptiles, birds, and arthropods.

Remarks.—The characters of the new genera and species described by Womersley are included in the Table, but are not discussed further because their full descriptions are included in this *Study*. The type genus is monotypic, *Apolonia tigipioensis* Torres & Braga 1938 being recorded from domestic fowls and also as causing scrub-itch in man. *Womersia* is likewise monotypic, *W. strandtmanni* being from a bird, U.S.A. *Shunsennia* Jameson & Toshioka 1953 is close to *Chatia* but differs in the fewer prongs to the palpal claw and the presence of an empodium. It includes the type *S. tarsalis* (with a tarsala III) and *Hannemania ochotona* Rad.

Since writing this, *Audyana thompsoni* Wom. 1953: 118 has been bred to the nymph, allowing it to be correctly placed in the Trombellinae, family Trombidiidae. Womersley has revised his paper accordingly, but before revision he had noted that all five genera described from larvae taken from arthropods may prove not to be apoloniine.

Old World species.—Africa: *Sauracarella africana*, *montana*, *whartoni* (all from reptiles). Asia and Pacific: *Shunsennia tarsalis* Jam. & Tosh., 1953 from a vole and mouse, Korea. *Cockingsia tenuipes* Wom., 1953 (this *Study* p. 115), from a beetle, Malaya. *Audyana thompsoni* Wom., 1953 (*idem*) from a scorpion, Malaya. *Grossia onychia* Wom., 1953 (*idem*) from a trombidiid, Australia. *Nothotrombicula deinacridae* Dumbleton, 1947 from an orthopteran, New Zealand. *Womersleyia minuta* Rad., 1946 from orthoptera, Maldives Islands, Indian Ocean.

FAMILY TROMBIDIIDAE LEACH

Diagnosis (incomplete, for comparison with that of Leeuwenhoeikiidae).—Larvae usually with more than one dorsal plate: an anterior scutum, frequently deep, dorsal to and obscuring the gnathosome; frequently with a postscutal plate bearing a pair of setae; usually with other dorsal plates bearing setae. Scutal setae usually 6 (anterior, intermediate, and posterior); usually bearing only 1 pair of filiform sensillae. Seta on pedipalpal coxa usually anterior to base of palpal femur. Legs 7-segmented, femora of legs being divided. Sternal setae usually multiple. Parasitic on arthropods, not on vertebrates. Nymphs and Adults often large (1-10mm): body cordate or pyriform broadest between legs II and III. Scutum with 1 (exceptionally 2) pairs sensillae (which may arise off the scutum); extending anteriorly to form an expanded plate which may project over the gnathosome as a tectum, bearing numerous setae (rarely the plate is absent and the scutum undeveloped); eyes if present may be 1+1, 2+2, sessile or pedunculated, placed away from the scutum. Most species of this family are known from the freelifving adult stage and not from the larval stage.

Comments on Checklist of Gunther, 1952

Gunther's checklist (1952) contains valuable references to literature and the location of type material. The early parts of the checklist were completed long before the publication date, as the author explains. It may be helpful to make a few comments as follows—the numbers in brackets refer to Gunther's page-numbers. The subfamily *Hemitrombiculinae* (pp. 2,24) was raised in error, *Hemitrombicula* Ewing being recognised later as a synonym of *Limnochares* Latreille, a hydrachnellid (vide Baker & Wharton, 1952:278). The genus *Nothotrombicula* Dumbleton is unrelated and is now placed provisionally by Womersley in the Apoloniinae sensu lato (Wom., 1953, this *Study* p. 108). As already noted (p. 156 above), the present writer believes it is premature to raise a subfamily Guntheraninae (p. 2) for the genus *Guntherana*, but this is only a matter of opinion. *Guntherana parana* (p. 2) is now synonymised by Womersley with the type *G. kallipygos*. In discussing the genus *Trombicula* (p. 3-4) the author is certainly correct in stating that it will take years to assign species to their subgenera, but this complete suppression of the tentative subgenera is equally certainly not a forward step.

T. mediocris (p.6) is the adult of *T. wichmanni* according to Womersley. Gunther records the breeding of nymphs of *T. hirsti* and the deposition of type and paratype in the South Australian Museum and the School of Public Health and Tropical Medicine in Sydney. Womersley does not however describe the nymph of this important scrub-itch chigger and the matter requires following up. Gunther (p. 5) in discussing the relationships between *hirsti* and *wichmanni* (which some workers would regard as subspecies or varieties) states that he "cannot concede their complete identity and is convinced that they are divisible at least into distinct subgenera. This will be discussed in (his) Part VI; meanwhile (he) is listing them as distinct species." The discussion referred to (p. 8) is a statement of opinion, expressed in a peculiar double negative which does not accord with the author's suppression of subgenera. No reasons are

given and the author's intention is not clear. On the same page he lists *hakei* which Womersley describes as a form of *hirsti*, not of *wichmanni*. *T. pseudoakamushi* (p. 12) is a synonym of *T. wichmanni*.

T. obscura (p. 15) has since been identified with *T. akamushi* by Womersley. As noted by Traub & Audy (1953, this *Study* p. 74) a form which appears to be very close to *obscura* is the dominant form of *akamushi* in North Borneo, where it occurs together with *deliensis*. Nymphs have been bred and an opinion on this form awaits further study. *T. keukenschrijveri* (p. 17) can be confirmed as a *Trombicula* (*Leptotrombidium*) in the *akamushi*-group. *T. hastata* (p. 18) is placed by the present writer in the subgenus *Trombiculindus*. On p. 21 line 20 *deliensis* is a *lapsus calamae* presumably for *mediocris*. Of the adults listed on pp. 21-22, *T. signata* is not a trombiculid but a *Podothrombidium* (vide Wom., 1952:312; it is also listed by Wharton & Fuller, 1952:70); *tindalei* and *translucens* are now placed in *Guntherana* (see p. 157 above). *T. chiroptera* (p. 22) is a synonym of *quadriense*. Of species listed under *Schöngastia* on p. 25, Womersley has identified both *katonis* and *pusilla* with *schuffneri*, while he omits all mention of *jamesi* (= *rotunda*, nom. nud.).

In dealing (p. 26) with the confusion of *Eu*—, *Neo*—, *Para*—, and *Ascoschöngastia*, the author states that he is taking the bull by the horns, but he is thrown in the wrong direction in his choice of *Neoschöngastia* which is the best-defined group and is therefore least suited to serve as a taxonomic dustbin. *Trisetica* (p. 37) is noted as fairly obviously a synonym of *Tecomatlana* but the authors of *Trisetica* have carefully discussed this very point. In connexion with the discussion of leeuwenhoekids on p. 38, the reader may be referred to Womersley, 1953 (this *Study* p. 108). The Walchiinae (Gahrlepiinae), p. 43-48, are in a fluid state and have already been discussed above.

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SUMMARY

1. The results of a preliminary study of some 130 species of trombiculid larvae and 70 species of nymphs from Malaysia are recorded. The conclusions are provisional but are made available to fellow-taxonomists because it will be many years before the available material can be fully studied and described. This paper is intended to be an appendix to the monographs by Womersley (1952) and Wharton and Fuller (1952).

2. The taxonomic importance is discussed of various characters, as listed in the Contents, and attention is drawn to certain characters which have been neglected. A possible course of evolution is given of similar species with different seasonal behaviour occurring together in the same country. The humeral, dorsal, caudal and ventral, and the various scutal, setae are believed to be influenced by different embryonic developmental fields, so that their differences are probably of more taxonomic importance than is usually supposed.

3. The classification of the trombiculids, at present based largely on the larval stage, will ultimately be based on postlarval as well as larval characters. Womersley's important study of the postlarval stages is a pioneer work; much still remains to be done. Our understanding of the taxonomic characters of the postlarval stages is considered to be still too undeveloped to allow stabilisation.

4. In the light of the Malaysian material, revised diagnoses (many of which are provisional) are given of the genera and subgenera of Old World chiggers, together with lists of those species from Europe, Africa, and the Asiatic-Pacific area which have been described by early 1953.

5. In addition to the accepted genera and subgenera, over 30 species groups are listed, at least three of which may deserve recognition as subgenera (viz. the *Euschöngastia indica*, *E. lacunosa*, and *Doloisia oculicola* groups).

6. The Trombiculinae are divided into two generic groups, related respectively to *Trombicula* and to *Euschöngastia*. The latter group has many affinities with the Gahrlepiinae (Walchiinae). The genera *Walchiella* (here treated as a subgenus of *Euschöngastia*, close to the *lacunosa*-group) and *Pseudoschöngastia* are considered to belong properly to the *Euschöngastia* complex and not to the Gahrlepiines.

7. The genus *Trombicula* sensu lato is revised and the subgenus *Trombicula* is based on the larval and nymphal characters of a new, undescribed bat-chigger which appears to be congeneric, if not identical, with the genotype *T. minor*. Evidence is offered to show that the postlarval stages of *T. minor* lack eyes. The subgenus *Leptotrombidium* is provisionally revised sensu lato; over 60 species are at present allocated to it.

8. *Fonsecia* is restored to generic rank and it is considered that the *T. ilei* group, which does not have modified scutal setae, may prove to be congeneric with it.

9. The genus *Euschöngastia* sensu lato is provisionally considered to comprise the subgenera *Euschöngastia*, *Walchiella*, and *Helenicula* n. subgen., together with the *indica*-group and the *lacunosa*-group which appear to be at least of subgeneric status but the limits of which cannot yet be defined. The *lacunosa*-group may possibly be identified with *Walchiella*, while the *indica*-group has close affinities with *Doloisia* sensu lato.

10. The genus *Doloisia* is treated sensu lato, comprising (a) the subgenus *Doloisia* sensu stricto, (b) a new subgenus (to be published), the larvae of which have PL setae off the scutum and the nymphs of which are very distinctive, resembling those of *Guntherana* and the Gahrlepiines in the shape of the scutum, and (c) an *oculicola*-complex which requires much further study. The larvae of *Doloisia* appear to have affinities with members of the *E. indica* group, and this requires further study.

11. The Gahrlepiinae (Walchiinae) are treated sensu stricto because they are a very distinctive group in both larvae and nymphs. The broad genus *Gahrlepieia* is considered to be the temporary repository of two or more groups which will later be given generic status. It is considered that the existing subgenera are based on false distinctions and that the subfamily needs drastic revision.

12. The Leeuwenhoekinae and Apoloniinae are hardly represented in the Indo-Malaysian collections, with the exception of *Whartonia* on bats. These subfamilies are briefly considered. Larval characters of the various genera are tabulated: Womersley's new genera, based on chiggers from arthropods and provisionally placed by him in the Apoloniinae, are included in the tabulation.

REFERENCES

- AUDY, J. R. (1947). Scrub typhus as a study in ecology. *Nature, Lond.*, 159, 295-296.
 AUDY, J. R. (1952). Trombiculid mites infesting bats in Malaya, with descriptions of three new species. *Bull. Raffles Mus.*, 24, 133-159.
 AUDY, J. R. (1953). Malaysian parasites. III—A summary review of collections of trombiculid mites in the Asiatic-Pacific area. *Stud. Inst. med. Res., Malaya*, 26, 29-44.
 AUDY, J. R. (1954). Malaysian parasites. New trombiculid species of taxonomic interest. *Stud. Inst. med. Res., Malaya* (in preparation).
 AUDY, J. R., THOMAS, H. M. AND HARRISON, J. L. (1953). A collection of trombiculid mites from Manipur and Lower Burma, 1945-1946. *J. Zool. Soc. India*, 5, 20-40.
 BAKER, J. A. AND WHARTON, G. W. (1952). *An introduction to acarology*. Macmillan, New York.

- BRENNAN, J. M. (1952). The genus *Pseudoschöngastia* Lipovsky, 1951, with the description of two new species, also *Neoschöngastia paenitens*, new name for *Neoschöngastia kohlsi*, Brennan, 1951, preoccupied. *Proc. ent. Soc. Wash.*, 54, 133-137.
- BRENNAN, J. M. (1952). *Trombicula cynos* Ewing, 1937 and three related species (Acarina: Trombiculidae) *Wasman J. Biol.*, 10, 55-65.
- BRENNAN, J. M. AND WHARTON, G. W. (1950). Studies on North American chiggers. 3. The subgenus *Neotrombicula*. *Amer. Midl. Nat.*, 44, 153-197.
- EWING, H. E. (1944). Note on taxonomy of type species of the mite genus *Trombicula* Berlese. *U.S. Nav. med. Bull.*, 43, 837-839.
- EWING, H. E. (1948). A note on the effect of engorgement on the arrangement of the dorsal abdominal setae in chiggers. *Proc. ent. Soc. Wash.*, 50, 85-88.
- FAIN, A. AND VERCAMMEN-GRANDJEAN, P. H. (1953). Les fosses nasales nouvelle localisation parasitaire des larves de Thrombidions chez les rongeurs. *Ann. Soc. Belge. Med. trop.*, 33, 41-42.
- FULLER, H. S. (1948). Some remarks on the Trombiculinae Ewing, 1929, in Das Tierreich, Trombidiidae, by Sig. Thor and Willmann. *Bull. Brooklyn ent. Soc.*, 43, 101-111.
- FULLER, H. S. (1952). The mite larvae of the family trombiculidae in the Oudemans collection: Taxonomy and medical importance. *Zool. Verh., Leiden*, 18, 1-261.
- FULLER, H. S. AND WHARTON, G. W. (1951). The generic names *Blankaartia* Oudemans, 1911, and *Trombiculoides* Jacot, 1938. *Psyche*, 58, 85-88.
- GISPEN (1950). The virus of murine typhus in mites (*Schöngastia indica*, fam. Trombiculidae). *Docum. neerl. indones. Morb. trop.*, 2, 225-230.
- GRANDJEAN, F. (1943). Le développement postlarvaire d' "Anystis" (Acarien). *Mem. Mus. nat. d'Hist. nat., Paris*, 18, 33-77.
- GRANDJEAN, F. (1947). Étude sur les Smarisidae et quelques autres Erythroïdes (Acarions). *Arch. Zool. exp. gen.*, 85, (1), 1-126.
- GREENBERG, B. (1952). A review of the New World *Acomatacarus*. *Ann. ent. Soc. Amer.*, 45, 472-491.
- GUNTHER, C. E. M. (1939). Trombidiid larvae in New Guinea. *Proc. Linn. Soc. N.S.W.*, 64, 73-96.
- GUNTHER, C. E. M. (1940). A survey of endemic typhus in New Guinea. *Med. J. Austr.*, 2, 564-573.
- GUNTHER, C. E. M. (1951). On *Trombicula minor* Berlese, 1905. *Proc. Linn. Soc. N.S.W.*, 76, 66-70.
- GUNTHER, C. E. M. (1952). A check list of the trombiculid larvae of Asia and Australia. *Proc. Linn. Soc. N.S.W.*, 77, 1-60.
- JADIN, J. AND VERCAMMEN-GRANDJEAN, P. H. (1952). Les trombiculides larvaires du Ruanda-Urundi. *Ann. Soc. Belge. Med. trop.*, 32, 593-656.
- JAMESON, E. W. AND TOSHIOKA, S. (1953). *Shunsennia tarsalis*, a new genus and species of chigger from Korea. *Proc. biol. Soc. Wash.*, 66, 89-92.
- JENKINS, D. W. (1949a). Trombiculid mites affecting man. III. *Trombicula* (*Eutrombicula*) *splendens* Ewing in North America. *J. Parasit.*, 35, 201-204.
- JENKINS, D. W. (1949b). Trombiculid mites affecting man. IV. Revision of *Eutrombicula* in the American hemisphere. *Ann. ent. Soc. Amer.*, 42, 289-318.
- JONES, B. M. (1951). The growth of the harvest mite, *Trombicula autumnalis* Shaw. *Parasitology*, 41, 229-248.
- LAWRENCE, R. F. (1949). The larval trombiculid mites of South African vertebrates. *Ann. Natal. Mus.*, 11, 405-486.
- LIPOVSKY, L. J. (1951). A new genus of Walchiinae. *J. Kans. ent. Soc.*, 24, 95-102.
- LIPOVSKY, L. J. (1952). A new genus and species of chigger mite. *J. Kans. ent. Soc.*, 25, 132-137.
- LOOMIS, R. B. AND CROSSLEY, D. A. (1953). A new species of chigger from Eastern Kansas. *J. Kans. ent. Soc.*, 26, 32-34.
- MICHENER, C. D. (1946). The taxonomy and bionomics of a new subgenus (*Megatrombicula*) of chigger mites. *Ann. ent. Soc. Amer.*, 39, 411-417.
- RADFORD, C. D. (1953). Four new species of "harvest-mite" or "chigger" and a new fur mite (Acarina, Trombiculidae and Liptrophoridae). *Parasitology*, 43, 210-214.
- REID, J. A. (1950). The *Anopheles umbrosus* group. Systematics, with descriptions of two new species. *Trans. R. ent. Soc. Lond.*, 101, 281-334.
- RICHARDS, W. S. (1950). The variation of the British harvest mite. *Parasitology*, 40, 105-117.
- TRAUB, R. AND AUDY, J. R. (1953a). Malaysian Parasites. IV—New species of *Trombicula* from Borneo. *Stud. Inst. med. Res., Malaya*, 26, 45-76.

- TRAUB, R. AND AUDY, J. R. (1953b). Malaysian Parasites. V—New species of *Euschöngastia* from Borneo. *Ibid.*, 77-88.
- TRAUB, R. AND EVANS, T. M. (1953). Malaysian parasites. VI—Indo-Malaysian Gahrlepiine mites of the subgenus *Schöngastiella* Hirst. *Stud. Inst. Med. Res., Malaya*, 26, 89-107.
- TRAUB, R. AND MORROW, M. L. (in preparation) Malaysian parasites: a revision of the subgenus *Gahrlepiea*. *Stud. Inst. Med. Res., Malaya*.
- TRAUB, R., FRICK, L. P. AND DIERCKS, F. H. (1949). Observations on the occurrence of *Rickettsia tsutsugamushi* in rats and mites in the Malayan jungle. *Amer. J. Hyg.*, 51, 269-273.
- VERCAMMEN-GRANDJEAN, P. H. (1952). Sur un nouveau trombiculidae larvaire de Ruanda-Urundi (Congo Belge). *Ann. Soc. Belge Med. trop.*, 32, 645-648.
- WHARTON, G. W. (1946a). Observations on *Ascoschöngastia indica* (Hirst, 1915). *Ecol. Monog.*, 16, 151-184.
- WHARTON, G. W. (1946b). The vectors of tsutsugamushi disease. *Proc. ent. Soc., Wash.*, 48, 171-178.
- WHARTON, G. W. (1950). Respiratory organs of chiggers. *Ibid.*, 52, 194-199.
- WHARTON, G. W. AND FULLER, H. S. (1952). A manual of the chiggers. *Mem. ent. Soc. Wash.*, 4, 1-186.
- WHARTON, G. W. AND HARDCASTLE, A. B. (1946). The genus *Neoschöngastia* in the western Pacific area. 32, 380-384.
- WILLMANN, C. (1941). *Trombicula minor* Berl. 1905, Typenart der gattung *Trombicula* Berlese (Trombididae, Acari). *Zool. Anz.*, 133, 131-136.
- WOLFENBARGER, K. A. (1952). Systematic and biological studies on North American chiggers of the genus *Trombicula*, subgenus *Eutrombicula*. *Ann. ent. Soc. Amer.*, 45, 645-677.
- WOLFS, J. AND VERCAMMEN-GRANDJEAN, P. H. (1953). Two trombiculid larvae from Costermansville (Kivu Province, Belgian Congo) of which one is a new species: *Schöngastiella wansoni* n. sp. *Parasitology*, 43, 207-209.
- WOMERSLEY, H. (1952). The scrub-typhus and scrub-itch mites of the Asiatic-Pacific region. *Rec. S. Aust. Mus.*, 10, 1-435. 118 pls.
- WOMERSLEY, H. (1953). Malaysian parasites. VII. New genera and species apparently of Apoloniinae (Leeuwenhoeekiidae), from the Asiatic-Pacific region. *Stud. Inst. med. Res., Malaya*. 26, 108-119.
- WOMERSLEY, H. AND AUDY, J. R. (1955). Malaysian parasites. Additions to the trombiculid fauna of the Asiatic-Pacific region. *Stud. Inst. med. Res., Malaya* (in preparation).
- WOMERSLEY, H. AND HEASLIP, W. G. (1943). The Trombiculinae (Acarina) or itch-mites of the Austro-Malayan and Oriental Regions. *Trans. Roy. Soc. S. Aust.*, 67, 68-142.